

ABSTRACT

Title of Document: ENVIRONMENTAL CONTROLS AND BIOLOGICAL CONSTRAINTS ON RECRUITMENT OF STRIPED BASS *MORONE SAXATILIS* IN CHESAPEAKE BAY

Edward J. Martino, Ph.D., 2008

Directed By: Professor Edward D. Houde,
Chesapeake Biological Laboratory,
University of Maryland Center
for Environmental Science

The causes of >30-fold recruitment variability in striped bass *Morone saxatilis* were investigated in Chesapeake Bay. Factors that affect survival and growth of early-life stages were evaluated through 1) field surveys in 2001-2003 to document spatial and temporal variability in larval and juvenile abundances, 2) synthetic data analyses to provide a longer-term perspective and 3) trophodynamic and growth analyses to document how environmental variability controls and regulates variability in year-class strength. Daily discharge from the Susquehanna River in spring months controlled the distribution and apparent survival of striped bass and other anadromous fish larvae. Control of recruitment in upper Chesapeake Bay includes both direct and indirect effects of hydrological variability on egg and larval survival. In dry years (1999 and 2002), direct effects of biophysical controls resulted in low abundances of striped bass feeding-stage larvae, a consequence of reduced retention of eggs and yolk-sac larvae at the salt front and Estuarine Turbidity Maximum (ETM). The

strongest year classes are produced in wet years that have high retention of eggs and yolk-sac larvae (i.e. direct effects), and a spatial and temporal match between feeding larvae and zooplankton prey (i.e. indirect effects). In moderate and high freshwater flow years (1996, 1998, 2001, 2003), indirect trophodynamic effects were most important. Striped bass larvae were strongly associated with the ETM in wet years when zooplankton prey levels also were highest in the ETM. A higher percentage of feeding larvae was observed in a wet year (2003) than in a dryer year (2001) (93% versus 35%) and faster larval growth (58% higher) occurred in the wet year. Inter-annual variability in growth and its effect on larval stage duration and cumulative mortality were sufficient to generate variability of the magnitude observed in juvenile recruitment. A forecasting model developed for age-0 striped bass recruitment that included spring flow and spring temperatures as independent variables has strong predictive capability. Growth of age-0 juveniles was density dependent, leading to diminished juvenile survival in years of high abundance through size-selective overwinter mortality. Through this mechanism, age-0 abundance levels that vary >10-fold are reduced to 3-4-fold variability at age-3. Density dependence regulates dynamics of age-0 juveniles, compensating for coarser controls over recruitment generated by environmental factors during the egg and larval stages.

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RECRUITMENT OF STRIPED BASS *MORONE SAXATILIS* IN CHESAPEAKE
BAY

By

Edward J. Martino

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Advisory Committee:
Professor Edward D. Houde, Chair
Professor Raleigh R. Hood
Professor Michael R. Roman
Professor Kenneth A. Rose
Professor David H. Secor
Professor Reginald Harrell, Dean's Representative

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DEDICATION

To my mom and dad.

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Many individuals helped to make this challenging goal possible, others made the experience enjoyable and a little easier.

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Figure 5-20. Chesapeake Bay striped bass recruitment process summarized with a modified Paulik diagram including both dominant environmental control at the larval stage and strong compensation at the juvenile stage.

Chapter 6

Figure 6-1. Conceptual illustration of controls of annual cohort abundance in Chesapeake Bay striped bass; a) without and b) with age-0 juvenile-stage density dependent growth and mortality acting as a regulator of year class strength.

CHAPTER ONE

General Introduction

The origins of biological oceanography are deeply rooted in a desire to understand causes of fluctuations in abundance of organisms in the sea. Pioneers of “recruitment thinking” (Hjort, 1914) recognized the strong link between environmental variability and early-life survival and recruitment of fishes (Kendall and Duker, 1998; Govoni, 2005). Not surprisingly, investigations of recruitment variability and processes contributing to it remain a prolific research topic in oceanography due, in part, to the current crises facing many of the world’s fishery and other marine resources (Baum et al., 2003; Myers and Worm, 2003).

Motivation for research on recruitment variability is to improve our understanding of causes of the >10-fold inter-annual variability in levels of recruitment and to develop a capability to predict year-class strength. One central question that must be answered to attain this goal is, “What causes fish population abundance to vary?” Numerous observations and examples demonstrate that either fishing mortality or environmental variability can be the primary cause of dramatic changes in fish population abundance. There is a long history debating the relative effects of natural environmental conditions versus fishing mortality (Walters and Collie, 1988; Hilborn and Walters, 1992). For example, the abundance of Atlantic cod *Gadus morhua* stocks in the Northwest Atlantic Ocean has declined since the 1960s due, in part, to overfishing. However, cod spawner biomass increased and then

decreased between 1975 and 1985 and 1985 and 1992, respectively, and both periods were associated with reduced fishing mortalities. The more recent decline in abundance has been attributed by some scientists to environmental conditions rather than overfishing (Rothschild, 2007). Similarly, the much publicized recovery of Atlantic coast striped bass *Morone saxatilis* apparently resulted from both reduced fishing pressure and favorable environmental conditions (Richards and Rago, 1999; Wood, 2000).

A second question that is crucial to understanding recruitment variability is, “At what life stage is recruitment variability generated?” The basis of “recruitment thinking” and research was the recognition of a ‘critical period’ occurring in larvae and during first feeding (Hjort, 1914). It is still generally accepted that high and variable mortality during the larval stage determines year-class strength in many populations of fish (Houde, 1989; Pepin and Myers, 1991). However, the first-feeding larval stage may not be the ‘critical period’ in all marine fish due to substantial variability in cumulative mortality beyond this stage of life that can determine the fate of year classes and levels of recruitment (Sissenwine, 1984; Bradford, 1992).

Density-dependent processes have the potential to regulate recruitment and to stabilize populations, especially when both density-dependent mortality and growth are operating (Houde, 1989). A long juvenile stage duration that is prolonged by density-dependent growth, combined with size-selective mortality, can generate high cumulative mortality that regulates year-class strength. The magnitude of mortality rates in late-larval and early-juvenile fishes is low compared to mortality rates of younger larvae (Houde, 1997). For example, instantaneous daily mortality rate of

Chesapeake Bay striped bass at early-larval stages averages 0.415 d^{-1} ($34\%\text{ d}^{-1}$), declines to 0.178 d^{-1} ($16.3\%\text{ d}^{-1}$) by the late-larval stage, and is only 0.009 d^{-1} ($0.9\%\text{ d}^{-1}$) by the juvenile stage (Houde, 1997). Still, the cumulative mortality during the long juvenile stage can be substantial and has the potential to determine year-class strength (Sissenwine, 1984). In North Sea plaice *Pleuronectes platessa*, density-dependent mortality of age-0 juveniles dampens variability in age-1 abundance (Ziljstra and Witte, 1985; Beverton and Iles, 1992). Further, a meta-analysis based on 17 populations of marine demersal fishes concluded that density-dependent mortality of juveniles is an important regulator of recruitment (Myers and Cadigan, 1993).

Density-dependent, compensatory processes must occur to impart resiliency and sustainability to exploited fish populations. Reliance on compensatory reserve is the historical basis of sustainable resource use and management. However, identifying and interpreting the degree of compensation can be controversial with respect to management advice because of the difficulty in demonstrating unambiguous evidence for density dependence (Rose et al., 2001). Evidence for density dependence can be strengthened if a process-level understanding of the mechanism is combined with careful analysis of field data and modeling (Rose et al., 2001).

A stock-recruitment relationship describes the number of progeny produced for a given level of adult spawners. This relationship, despite its variability, is used by managers to evaluate alternative harvesting strategies and, especially, to determine the level of fishing that reduces spawning stock biomass to a point below which a population is likely to collapse. However, the relationship is difficult to interpret for most stocks due to the effects of stochastic, environmental variability on early life

survival, and striped bass is no exception. Age-0 juvenile recruitment and spawning stock abundance indices from upper Chesapeake Bay have been fit to Ricker stock-recruitment models, both with and without freshwater discharge that has been shown to be a strong environmental predictor of recruitment (North and Houde, 2003). The Ricker model fit without freshwater discharge explained only 3% of the variance in recruitment while the model incorporating freshwater discharge explained an additional 41% of the variance. Such modeling results highlight the importance of hydrological conditions as a coarse controller of striped bass recruitment variability. While the strong relationship between meteorological and hydrological conditions and striped bass recruitment variability has been recognized for decades (Merriman, 1941), the mechanisms and processes involved are poorly known.

One major goal of my dissertation was to identify mechanisms and processes that would substantially enhance understanding of larval survival and recruitment variability in striped bass. Previous research had evaluated effects of variable environmental conditions in Chesapeake Bay on weekly egg and larval cohort survival (Rutherford and Houde, 1995; Secor and Houde, 1995; McGovern and Olney, 1996). My dissertation research places particular emphasis on inter-annual variability in biophysical controls, hydrological conditions, and associated spatial variability in processes that control larval survival and subsequently affect juvenile recruitment. Recent research has indicated a link between survival of anadromous fish larvae and the structure and dynamics of the estuarine turbidity maximum (ETM) and salt front in upper Chesapeake Bay (North and Houde, 2001; North and Houde, 2003) and in the St. Lawrence River estuary (Dodson et al., 1989; Laprise and Dodson, 1989; Laprise

and Dodson, 1990; Sirois and Dodson, 2000a; Sirois and Dodson, 2000b). My analyses depend on data from three years of new field research, but also include data from earlier research on the role of the ETM in fish recruitment. Major objectives of my dissertation were to analyze and evaluate striped bass recruitment variability using a combination of 1) field surveys to document spatio-temporal variability in abundances, 2) synthetic data analyses to provide general understanding of processes operating on striped bass larval and juvenile stages, and 3) feeding and growth analyses to explicitly determine how trophodynamic processes in early life generate variability in year-class strength.

My primary goal was to evaluate the recruitment process holistically across early-life and juvenile stages in striped bass. Most research on Chesapeake Bay striped bass recruitment has focused on egg and larvae survival, with minimal consideration of processes operating at the juvenile stage. However, research in the San Francisco Bay estuary (Kimmerer et al., 2000) and Hudson River (Hurst and Conover, 1998) indicated that processes in the juvenile stage could be important in controlling recruitment. My results provide new insight and understanding of how larval-stage dynamics and trophodynamics are linked to dynamics and density-dependent regulation of recruitment at the juvenile stage.

The dissertation is presented in five chapters. In Chapter 2, I describe ichthyoplankton assemblages and report on distribution patterns of dominant ichthyoplankton in upper Chesapeake Bay. My analysis is based on surveys during May of 2001, 2002, and 2003, three years characterized by strong contrasts in hydrological conditions and recruitment success of anadromous species, including

striped bass. Taxa included in the larval community analysis are predominantly anadromous species that comprised over 90% of ichthyoplankton abundance during the research surveys. Results are discussed considering multispecies and taxon-specific recruitment patterns and their relationship to climate variability and hydrodynamic forcing.

In Chapter 3, distribution and abundance of striped bass larvae and of zooplankton that serve as prey for larvae were evaluated with respect to environmental gradients during May of three years (2001-2003) under variable hydrological conditions. The specific objectives of this chapter were to provide evidence that annual hydrological conditions control the locations where striped bass larvae and zooplankton are most concentrated in the upper Chesapeake Bay. I also evaluated whether or not larvae overlap temporally and spatially with sufficient zooplankton prey resources. An analysis of striped bass larval diets was conducted to support findings

In Chapter 4, growth rates and growth-rate variability of larval-stage striped bass were analyzed based on daily increments in otolith microstructure. Measures of larval growth alone may not be sufficient to explain or predict recruitments but growth and growth-related factors are often correlated with recruitment potential (Houde, 1997). Growth of larval striped bass among years was evaluated with respect to feeding-stage larval abundance and year-class strength in upper Chesapeake Bay. I also evaluated size- and growth-selective mortality by comparing size and growth rates between the average larval population and larval survivors sampled at a later date. Growth rates were estimated using both ‘cross-sectional,’ population-based and

‘longitudinal,’ individual-based approaches. Variability in growth rates was interpreted with respect to environmental and hydrological conditions, and implications for larval survival and recruitment variability are discussed.

The results of Chapters 1 through 4 suggested that biophysical controls have both direct and indirect effects on survival of striped bass early-life stages. Direct effects consist of down-estuary loss of eggs and yolk-sac stages, and these effects are most prevalent when freshwater flows and gravitational circulation are reduced. When freshwater flows are low, a weaker convergence due to reduced gravitational circulation, combined with higher salinities in the ETM, leads to increased buoyancy of striped bass eggs and larvae that may increase egg and larvae losses down-estuary (North and Houde, 2006). These direct effects of biophysical controls are probably important to distinguish very poor from moderate year classes, such was the case in 1998 and 1999 when recruitments of striped bass were average and poor, respectively (North and Houde, 2001; Martino et al., 2006).

Indirect effects of biophysical controls of striped bass larval survival involve trophodynamic processes and effects of annual differences in prey abundance as well as differences in the spatial and temporal overlap of prey with larvae. These indirect effects only affect feeding-stage larvae and are probably most important to distinguish moderate (1998, 2001) and strong (1996, 2003) year classes. The wet conditions that occurred in 1996 and 2003 were associated with high feeding-stage larval abundances that overlapped temporally and spatially with zooplankton prey and, consequently, larval feeding success, growth, and survival were enhanced. The cumulative results of indirect and direct effects define the recruitment process to the age-0 juvenile stage.

In Chapter 5, I evaluated how growth and survival of age-0 juveniles vary relative to larval-stage abundances and how age-0 dynamics regulate recruitment variability in older juveniles (age 1+) and adults. Retrospective, time-series analysis applied to data on age-0 juvenile sizes revealed that lengths attained at the end of the first growing season and growth rates were lower when age-0 abundance was high. Further, mortality rates of age-0 juveniles throughout the first year of life are lowest when juvenile abundance is low. My analyses on juvenile diets, benthic prey availability, and bioenergetics-based consumption demand support new findings and conclusions that density dependence contributes importantly to regulation of year-class strength of striped bass in Chesapeake Bay.

Other factors such as maternal effects and predation are not addressed in my research but also are possible regulators of recruitment variability. Maternal effects including the influence of spawner age structure on offspring size and the timing of offspring production could be important. Spawner age diversity was positively correlated with the length of the spawning period by striped bass during the population's recovery period (1985-1995) (Secor, 2000) and with recruitment success (Houde 2008). Minority spawning behaviors may be important to reduce the probability of mis-timed egg production that adversely affects larval survival. Predation is a major source of mortality in the early life of fishes (Bailey and Houde, 1989). Annual differences in the magnitude of predation mortality on striped bass early-life stages could certainly affect strength of recruitment in Chesapeake Bay. Findings in my dissertation highlight the importance of biophysical controls of variability in larval survival and regulation of recruitment through density-dependent

juvenile mortality. However, the complete recruitment process is complex and other factors are important.

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CHAPTER TWO

Effects of hydrological variability on composition, abundance, and distribution of ichthyoplankton in upper Chesapeake Bay

INTRODUCTION

The low-salinity (salinity range 0-11) areas of the upper Chesapeake Bay are recognized as critically important nursery habitat for many anadromous, estuarine, and coastal-spawning marine fishes, where over 95% of fish larvae occur in salinities under 11 and over 75% occur in salinities under 7 (Dovel, 1971). A consistent finding in previous research on ichthyoplankton in the upper Bay was the dominance of two taxonomic groups, the moronids, represented by striped bass *Morone saxatilis* and white perch *M. americana*, and alosines, represented by blueback herring, *Alosa aestivalis*, alewife, *A. pseudoharengus*, hickory shad *A. mediocris*, and American shad, *A. sapidissima*. Ichthyoplankton in the upper Bay and tributaries has been studied and described in the past three decades (Dovel, 1971; Mihursky et al., 1981; Rutherford, 1992; Campfield 2004) but not in a detailed evaluation relative to hydrography and hydrologic variables that influence occurrence, abundance, and distribution.

Hydrological control over biological productivity in estuarine ecosystems has been recognized in other estuaries. For instance, the position of the 2 isohaline in San Francisco Bay predicts levels of productivity for many organisms across multiple

trophic levels (Jassby et al., 1995; Kimmerer, 2002). This may also be true for populations associated with the salt front and estuarine turbidity maximum (ETM) in upper Chesapeake Bay, including organisms from many taxonomic groups and trophic levels, ranging from mesozooplankton (Roman, 2001; Lloyd, 2006) to anadromous fish (Wood, 2000; North and Houde, 2003).

The ETM is a dominant physical feature of coastal plain estuaries. In the upper Chesapeake Bay and its tidal tributaries during spring, the ETM is located near the salt front (Schubel, 1968). Its location usually is near where the 1.0 salinity isohaline intersects the bottom but its position can shift with level of freshwater discharge and in response to episodic flow and wind events (North et al., 2004; North et al., 2005). The upper Bay's ETM is known to provide favorable nursery habitat for striped bass and white perch larvae (North and Houde, 2001, 2003; Martino and Houde, 2004), possibly because concentrations of the copepod *Eurytemora affinis*, a common prey of striped bass larvae, are elevated in and near the ETM (Boynton et al., 1997; North and Houde, 2001; Roman et al., 2001; North and Houde, 2006). A substantial portion of striped bass eggs and larvae, and white perch larvae, are transported to and retained within the ETM where their survival is enhanced (North and Houde, 2001, 2003, 2006).

Inter-annual variability in abundance of young fishes has been linked to spring months synoptic climatology and resulting hydrological variability (North and Houde, 2001; Wood, 2000; Jung and Houde, 2002; North and Houde, 2003; Martino and Houde, 2004). Research on climatologies revealed a positive relationship between freshwater flow and recruitment of anadromous fishes (Wood, 2000), including striped

bass (McGovern and Olney, 1996; North and Houde, 2001; Wood, 2000; North and Houde, 2003; Martino and Houde, 2004). My preliminary results confirmed this relationship and degrees of larval overlap with zooplankton prey (Chapter 3). The complex biophysical controls explaining these relationships are still being investigated. Understanding mechanisms underlying striped bass recruitment variability and effects of hydrologic conditions could enhance our understanding of how freshwater flow affects not only recruitment of striped bass but also other anadromous fishes.

Objectives of this chapter are to describe effects of inter-annual hydrological variability on the abundance, distribution, and spatial overlap of dominant ichthyoplankton in upper Chesapeake Bay. The research was undertaken during three years characterized by very different hydrological conditions and, as such, presented a promising opportunity to evaluate effects of hydrological variability on these organisms. A particular emphasis is placed on striped bass because the broader research program (NSF-BITMAX) focused on this species and our research cruises were planned to coincide with the seasonal peak in larval striped bass occurrence. I hypothesized that the distribution and abundance of feeding-stage larvae of striped bass is controlled by annual hydrological conditions, and that in wet years larvae of all taxa are more abundant and occur further down-estuary. The potential for inter-specific competition and larval-stage interactions that potentially may control or regulate recruitment are considered.

MATERIALS AND METHODS

Research Surveys

Research surveys were conducted in the upper Chesapeake Bay (Figure 2-1) from the 50-ft RV *Orion* and 120-ft RV *Cape Henlopen*. Collections were made during the NSF-funded BITMAX project in May 2001, 2002 and 2003. The locations of the ETM and salt front were determined in each survey from CTD casts in a hydrographic survey along the channel axis of the upper Bay. Based on the hydrographic surveys, stations were selected to map gradients in ichthyoplankton abundances above, within, and below the ETM and salt front (Figure 2-1). In addition to CTD casts during the hydrographic survey, the CTD was deployed at each station prior to ichthyoplankton sampling. Turbidity measurements in 2001 and 2002 were recorded in NTU units in 2001 and 2002 and in transmittance units in 2003. The channel survey area averaged approximately 13 m in depth. The water column was divided into surface, middle, and bottom layers and environmental variables were averaged for each layer to coincide with Tucker trawl samples from those depths.

Ichthyoplankton was sampled with an opening-closing, 1-m² Tucker trawl with 280-um meshes at three discrete depths. The mean volume filtered by a 2-min tow was 126 m³. All striped bass, white perch, alosine, cyprinid, and less common freshwater taxa eggs and larvae were removed from samples, identified, and enumerated, and expressed as numbers per cubic meter. Table 2-1 summarizes collection and survey information.

All analyses are based on abundances of yolk-sac and feeding stages of striped bass, white perch, alosine, and cyprinid larvae. The four potential alosine species were grouped as “aloses” because, with the exception of American shad *A. sapidissima*, their identification in the larval stage is difficult and uncertain. Preliminary multivariate analyses were run with American shad treated separately; these analyses revealed that American shad generally responded to environmental gradients in a manner similar to the alosine group at large.

Abundances of juvenile fish were estimated from catches in a midwater trawl during July and October in each of the three years. The midwater trawl was towed obliquely from the surface and stepped down to the bottom at 2-min intervals for a total tow time of 20 minutes. The trawl’s mouth opening is 18 m² and its codend mesh size is 6 mm. All collected fish, or subsamples when abundant, were measured and weighed immediately, and either discarded, frozen, or preserved in ethanol. Abundances of juvenile fish were analyzed and related to their larval distributions to determine if there is a linkage between larval-stage abundance and age-0 recruitment.

Statistical Analyses

Annual and spatial variability in ichthyoplankton assemblages from the upper Bay was evaluated using both univariate and multivariate statistical analyses. Statistical analyses included an evaluation of abundances of individual species and life stages across a suite of abiotic factors. Generalized additive models (GAMs) were applied to determine variability in species distributions and spatial co-occurrences, and

to determine what factors best explain patterns in abundance and distribution. Secondly, a multivariate assemblage analysis was conducted using samples from the three years combined to identify key differences in broad taxonomic composition and environmental determinants of assemblage structure among years. Thirdly, multivariate assemblage analyses on samples within years were undertaken to synthesize findings on distribution of individual species and to identify spatial patterns in larval assemblages during years characterized by different hydrological conditions.

The multivariate assemblage ordination was a direct gradient analysis, Canonical Correspondence Analysis (CCA), to identify assemblages and to link assemblages with important environmental factors between and within years (ter Braak, 1987). Direct gradient analyses explain the link between abiotic and biotic factors and limit the results to linear combinations of measured abiotic variables. Salinity, temperature, dissolved oxygen, turbidity, and distance downbay were included in the direct gradient analyses. Sample depth was not directly included in the analyses. But, samples were coded for sample depth (bottom, mid, surface) to assist in interpretation of results and to identify possible depth affinities of taxa.

Generalized additive models (GAMs) were applied to analyze patterns in yolk-sac and feeding-stage larvae distributions, and to identify important determinants of distribution. GAMs, rather than more traditional parametric statistics, are being used increasingly in recent years because of their flexibility compared to traditional linear models. Generalized additive models (GAMs) relax the normality and linearity assumptions inherent to general linear models (GLMs) and, instead, utilize non-parametric smoothing functions (Hastie and Tibshirani 1990; Swartzman et al. 1992;

(Maravelias, 1997, 1999)). The power of GAM models generally exceeds performance of conventional regression techniques. Probability distributions for the data can include any exponential form including normal, Poisson, and binomial (Swartzman et al., 1992). The smoothing during GAM model fitting and model flexibility increase with available degrees of freedom.

I applied a two-stage GAM analysis. First, GAM models were used to provide smooth fits to larvae distribution data using only a location variable (distance downbay, km) to identify general spatial trends in larvae occurrence. In this step, the least squares estimate of traditional regression techniques was replaced by a local smoother, the cubic spline smoother (Hamming, 1973). This first step was followed by a more rigorous analysis of factors responsible for patterns in larvae abundance. The second step adopted a widely used GAM fitting methodology, a backward selection process using a combination of individual predictor p-values, an overall measure of model goodness of fit based on Akaike's information criteria (AIC), and visual inspection of the conditional effects of each variable considered. The AIC statistic takes into account degrees of freedom and number of parameters in the model, such that models with more parameters will be penalized more than less complex models (Chambers, 1992).

$$AIC = -2 \cdot LLF + (2 \cdot N)$$

LLF = Log-likelihood function

N = Number of parameters in model

The selection process for GAMs was initiated by modeling distributions of feeding- and yolk-sac- stage larvae using the full suite of independent variables

including distance downbay (DB.DIST), salinity (SALT), temperature (TEMP), turbidity (TURB), dissolved oxygen (DO), and sampling depth (DEPTH). Variables were iteratively eliminated from a GAM if all of the following criteria were met: 1) the p-value of a variable was high (approaching 1), 2) the standard error of conditional effects overlapped zero throughout the entire range of a variable, and 3) model fit improved, i.e., reduction of model AIC, when the variable was removed. Final model AIC for each species and stage, and p-values for individual predictor variables were reported. Significant conditional effects for salinity, turbidity, and depth were plotted for each taxon.

RESULTS

Environmental Variability Among Years

Research surveys were conducted in three years characterized by very different spring hydrological conditions (Figure 2-2). Freshwater flows from the Susquehanna River during March and April were somewhat below average in 2001 (19% below 30-yr average), were considerably lower in 2002 (42 % below 30-yr average), and were above average in 2003 (17% above 30-yr average). Mean salinity during research cruises, averaged over all depths at the locations surveyed, were 1.78, 2.12, and 2.46 in 2001, 2002, and 2003, respectively, and mean temperatures were 18.96, 17.37, and 16.46 °C during those years (Table 2-2).

Species Composition and Inter-Annual Patterns in Abundance

The upper Bay ichthyoplankton was dominated by two major taxonomic groups including two moronids, the striped bass and white perch; and, four alosines, the blueback herring, alewife, hickory shad, and American shad. Freshwater cyprinids, referred to here as Cyprinidae, included spottail shiner *Notropis hudsonius*, satinfish shiner *Notropis analostanus*, golden shiner *Notemigonus crysoleucas*, and silvery minnow *Hybognathus regius*. The Cyprinidae were important as a group but were less abundant and occurred less frequently than the alosines and moronids (Figure 2-3). Other freshwater taxa included yellow perch *Perca flavescens*, the quillback sucker *Carpionodes cyprinus*, and freshwater darters *Etheostoma spp.*, although they were much less important than the moronids and alosines in both numbers and frequency of occurrence. The low taxonomic diversity contrasted with relatively high larval fish abundances that exceeded 40 larvae m⁻³ at some stations and times.

Total ichthyoplankton concentrations varied considerably among years. Mean concentrations of feeding-stage larvae summed over all species and taxonomic groups were 8.85, 1.28, and 16.71 larvae m⁻³ in 2001, 2002, and 2003, respectively (Table 2-1), and were clearly lowest in 2002. Mean concentrations of total yolk-sac larvae were 3.89, 3.08, and 8.25 in 2001, 2002, and 2003, respectively. Variability in feeding-stage larvae concentrations was high, with standard deviations of 12.63, 2.32, and 20.31 in 2001, 2002, and 2003, respectively (CVs = 143%, 181%, and 122%,

respectively). Concentrations of yolk-sac larvae also were variable, with standard deviations of 4.44, 4.44, and 8.55, respectively (CVs = 114%, 144%, and 104%, respectively).

Assemblage Structure Between Years

The spring ichthyoplankton assemblage exhibited conspicuous inter-annual variability in response to differing hydrological conditions. Taxa dominance differed among years. Alosines were dominant in 2001; fish larvae were uncommon in 2002 although there were frequent occurrences of cyprinids; and, moronids were dominant in 2003 (Figure 2-3). The canonical correspondence analysis (CCA) (Figure 2-4) identified three distinct assemblages, one representing each year. The environmental variables explained 30% (0.40/1.34) of the variation in ichthyoplankton assemblages, and the first two CCA axes explained 25 % of the total variation (Table 2-3).

In 2001, the ichthyoplankton was dominated by alosines, including American shad and blueback herring. There were lower numbers of striped bass and white perch in 2001 (Figure 2-4). During 2002, a dry year, all common taxa at feeding stage were much less abundant than in the other two years (Figure 2-4). Striped bass eggs and, surprisingly, freshwater cyprinid larvae were the most conspicuous members of the assemblage in 2002 (Figure 2-4). During 2003, a wet year, abundances of striped bass and white perch larvae were very high (Figure 2-4). The dominance of white perch in 2003 was most evident at the feeding stage, but both yolk-sac and feeding-stage larvae of striped bass were dominant in 2003. The abundances of feeding-stage striped bass

and white perch larvae were approximately 30-fold and 20-fold higher, respectively, in 2003 than in 2002 (Figure 2-3).

The environmental variability during this 3-year study explained a considerable proportion of variation in annual ichthyoplankton taxonomic composition and abundance (Table 2-3)(Figure 2-4). Temperature (-0.93) and dissolved oxygen (+0.76) were most correlated with CCA axis 1 whereas only downbay distance (-0.50), and to a lesser extent salinity (+0.19) and dissolved oxygen (+0.19), were most associated with CCA axis 2 (Figure 2-4). Alosines (Asp) best defined the 2001 assemblage, based on negative species loadings across axis 1. The environmental loadings in this ordination indicated that 2001 samples were associated with higher temperatures and lower dissolved oxygen levels compared to the other two years. Ichthyoplankton in 2003 was characterized by high abundances of feeding-stage striped bass (SB.fd), yolk-sac striped bass (SB.ys), and feeding-stage white perch (WP.fd) larvae (Figure 2-4). Moderate temperatures, lower salinities, and higher larvae abundances down-estuary were associated with the environment supporting the 2003 assemblage (Figure 2-4). The ichthyoplankton assemblage in 2002 was generally depauperate across all taxa, but on a relative basis the importance of white perch yolk-sac larvae, striped bass eggs, and cyprinid feeding-stage larvae were high. Environmental loadings in 2002 reflected higher salinities, and higher abundances of larvae further up-estuary compared to the other years.

Species and Stage-Specific Distributions

There were annual differences in the distribution of species and life stages across the upper Bay's ETM and estuarine transition zone. The initial GAMs using downbay distance exclusively as a predictor of larvae concentrations provided smooth curves of species distributions along with standard errors. In general, in 2001 and 2003 abundance across all species was highest within and up- estuary of the salt front and ETM and usually declined precipitously below the salt front and ETM. Fish larvae concentrations fell off rapidly at sites more than 10 km below the ETM where salinities usually exceeded 5 (Figure 2-5 and Figure 2-6). In contrast, the distribution of all stages and taxa in 2002 extended well below the salt front and ETM.

The position of the ETM and salt front appeared to exercise control over larval distributions. The centers of larval abundance for each of the taxa varied among years and also differed by life stage. For example, well-defined centers of abundance of yolk-sac larvae of all taxa occurred upbay when annual freshwater discharge was close to normal (2001), and further downbay in the wet year (2003) (Figure 2-5). Striped bass yolk-sac and feeding-stage larvae had conspicuous centers of abundance just up-estuary of, or in, the ETM in 2001 and 2003. In contrast, yolk-sac stages of white perch and alosine larvae occurred further upbay in 2001 and 2003 (Figure 2-5), while feeding-stage larvae of these two taxa were more associated with the ETM (Figure 2-6). However, distribution of alosine larvae in 2003 was not precisely defined compared to their distribution in 2001 and to the distribution of striped bass and white perch in 2003. During 2002, when spring freshwater discharge was very low,

distribution patterns of all taxa differed substantially, with equal proportions of feeding larvae (Figure 2-6) and higher proportions of yolk-sac larvae (Figure 2-5) occurring below the salt front.

Striped bass eggs were not included in the GAM modeling that focused on larvae, but eggs usually occurred upbay of the locations of maximum concentrations of feeding-stage and yolk-sac larvae. Still, striped bass eggs were broadly distributed across the upper Bay. Importantly, feeding-stage abundances of striped bass and white perch larvae were much higher in 2003 when they were most associated with the ETM and salt front in a narrow distributional range.

In the second analysis, GAMs were constructed for each species using all variables determined to be important on a species by species basis. This analysis facilitated determining what factors were responsible for observed distribution patterns for each species or taxonomic group and how species responded to different levels of the important variables. In general, downbay distance, salinity, and depth at which samples were collected were the most important factors determining distribution of ichthyoplankton. Salinity and downbay distance were important in GAM models for all taxa in at least one year (Table 2-4).

The effect of salinity on larval distributions varied among years and highlighted the importance of annual hydrological conditions. Larval moronids were associated with very low salinities (0-2) in 2001 and 2003, the moderate and high freshwater-flow years, respectively. Maximum concentrations of yolk-sac and feeding alosine larvae also peaked at very low salinities or in freshwater in 2003. In contrast, in 2002 when conditions were dry, larval moronids had concentration peaks at higher

salinities of 3-8 (Figure 2-7). These higher-salinity associations are indicated by positive conditional probabilities at salinity of 5 for feeding-stage larvae and 3 and 7 for yolk-sac larvae (Figure 2-7). Further, the conditional effects of salinity are apparent after the effect of downbay distance has been removed, and thus indicate association of moronid larvae with the salt front and ETM rather than an artifact of collinearity between salinity and distance downbay.

The importance of sampling depth on occurrences and abundance varied among species, life stages, and years although several generalities were apparent (Table 2-4). Larval striped bass and white perch concentrations increased with sampling depth, indicating increased concentration in mid- and near-bottom samples for yolk-sac and feeding stages of striped bass in 2001 and 2003, but not in 2002 when abundances were lower (Figure 2-8). Alosine larvae were usually more abundant at surface and mid depths. The concentrations of feeding alosine larvae in 2001 and yolk-sac alosine larvae in 2002 and 2003 were higher at the surface, but yolk-sac alosine concentrations increased with depth in 2001 (Figure 2-8).

Turbidity sometimes was an important predictor. The response in larval abundance to turbidity was usually positive, with maximum concentrations of larvae predicted at moderate to high turbidity levels (Figure 2-9). One exception was the highest concentration of yolk-sac alosines observed at low turbidities in 2003. Moronid larvae were associated with moderate to high turbidities only during 2002 (Figure 2-9), the dry year, when larvae tended to occur below the ETM and at higher salinities (Figure 2-6 and Figure 2-7).

Temperature and dissolved oxygen also were important for some taxa in some years. The relationship between larval concentrations and oxygen was not always positive, suggesting that oxygen may have covaried with other unmeasured variables such as primary production and respiration, or that oxygen levels were always above a threshold where it was not an important determinant of larval distribution.

Cyprinid occurrences were sporadic and not often associated with environmental variables in the GAMs. Abundance of larvae of freshwater minnows, the Cyprinidae group, which could not be identified to genus or species, may have included spottail shiner *Notropis hudsonius*, satinfin shiner *Notropis analostanus*, golden shiner *Notemigonus crysoleucas*, and silvery minnow *Hybognathus regius*. Abundances were low, probably because the study location was downbay from freshwater spawning areas. Nonetheless, the few identified environmental relationships seem reasonable for freshwater species (Table 2-4). Important environmental relationships for cyprinids included negative relationships with downbay distance and salinity, and a positive relationship with dissolved oxygen in 2001, 2002, and 2003, respectively.

Species Overlap

Species overlap also varied among years. Spatial overlap was considerably higher in 2003, the wet year, when abundances were very high, and when the ETM, salt front, and center of abundance for most ichthyoplankton shifted downbay (Figure 2-10). Spatial overlap of taxa and the possibility for species interactions were high for

some species combinations but the potential interactions were variable among years (Figure 2-10). Not surprisingly, taxa exhibited peak concentrations at different locations along the salinity gradient (Figure 2-6).

Striped bass and white perch concentrations across all locations were significantly correlated in two of the three years (Figure 2-10a). In 2001, they overlapped to a moderate degree ($r = +0.47$ $p < 0.001$); they did not overlap significantly in 2002; and in 2003, when larvae were most abundant, the overlap was highest ($r = +0.78$ $p < 0.001$) (Figure 2-10g).

Striped bass and alosine concentrations were not significantly correlated in 2001 and 2002, the moderate and low freshwater discharge years, but were significantly correlated ($r = +0.46$ $p < 0.05$) in the wet year 2003. There were significant correlations between alosines and white perch larvae in 2001 ($r = +0.57$ $p < 0.001$) and 2003 ($r = +0.51$ $p < 0.01$).

In general, maximum overlap of taxa occurred in 2003 when freshwater discharge was above average. Species overlap was most prevalent near the salt front compared to overlap up- or downbay (Figure 2-6). Notably, the only significant correlations between species pairs occurred (Figure 2-10) during 2001 and 2003, years when taxa were most associated with the salt front (Figure 2-5).

The degree of overlap was reduced when depth-specific abundances of taxa were analyzed. In 2001 and 2003, correlations between striped bass and white perch were similar (2001: $r = +0.47$ reduced to $r = +0.46$; 2003: $r = +0.81$ reduced to $r = +0.78$) when depth-stratified samples were analyzed because the two species occurred most often at bottom depths. In contrast, the correlation between white perch and alosines

was reduced substantially when compared on a depth-specific basis (2001: $r=+0.57$ reduced to $r=+0.45$; 2003: $r=+0.51$ reduced to $r=+0.32$) because alosines primarily occurred in surface waters.

Assemblage Structure Within Years

A multivariate assemblage analysis provided a synthesis of findings of the single-species GAM modeling and integrated taxa-specific responses across spatial gradients within years. Variability in assemblages within years generally resulted from species responses across spatial-environmental gradients because ichthyoplankton was collected only in May. Thus, environmental relationships in ordinations each year represent effects of spatial gradients in abiotic factors (Figure 2-11, 2-12, and 2-13) in contrast to the inter-annual multivariate analyses that revealed broad inter-annual patterns (Figure 2-4).

Based on percentage of variation explainable along the first two ordination axes, the strength of intra-annual environmental effects was similar in magnitude to the strength of inter-annual environmental effects. The percentage of intra-annual variation that could be explained by abiotic factors varied among years. During 2001, 2002, and 2003, the first two CCA axes explained 27%, 20%, and 30% of variation in assemblage structure, respectively (Table 2-5, Table 2-6, and Table 2-7). This outcome suggests that the effect of environmental spatial gradients on assemblage structure was less pronounced when freshwater discharge was low (2002).

Two assemblages were revealed in the CCA ordination for 2001 (Figure 2-11) when turbidity, temperature, salinity, and downbay distance were important determinants of assemblage structure with CA axis 1 scores of -0.80, +0.59, -0.55., and +0.16 respectively, and CA axis 2 scores of +0.20, -.42, +0.52, and +0.96, respectively. In 2001, moronid yolk-sac and feeding-stage larvae occurred predominantly at upbay stations and tended to occur at mid to bottom depths where turbidity levels were higher. Alosine yolk-sac larvae were associated with warmer temperatures. Feeding stages of alosines and Cyprinidae larvae defined an assemblage that occurred predominantly in the surface layer at lower salinities, lower turbidities, and warmer temperatures (Figure 2-11).

During 2002, assemblage variability was less clear (Figure 2-12). In this year, turbidity, temperature, and dissolved oxygen were important determinants of assemblage structure. These three variables were correlated with CCA axis 1, with scores of +0.76, +0.55, and -0.55, respectively, while turbidity and temperature were correlated with axis 2, with scores of -0.47 and +0.42, respectively. Downbay distance was less important in 2002 than in 2001 or 2003, presumably a response to lower freshwater discharge levels and associated reduction in habitat, and an upbay shift in the distribution of ichthyoplankton (Figure 2-5 b,e,h). White perch yolk-sac and feeding-stage larvae, striped bass yolk-sac larvae, and Cyprinidae larvae were associated with high salinities and high turbidities in 2002, while alosines occurred further downbay and were most prevalent in lower-salinity surface waters (Figure 2-12). Few feeding-stage larvae of striped bass were collected during 2002, and those few individuals that were collected were further downbay than other taxa.

During 2003, there was a distinct assemblage of striped bass yolk-sac and feeding-stage larvae and white perch feeding-stage larvae (Figure 2-13). Freshwater discharge was above average in 2003 (Figure 2-2) and temperatures were cool compared to 2001 and 2002 (Table 2-2). Turbidity and downbay distance were most correlated with CCA axis 1 with scores of +0.73 and +0.84, respectively, while salt and temperature were most correlated with CCA axis 2, with scores of +0.59 and -0.58, respectively. The assemblage occurred further downbay in 2003 than the locations of moronid feeding larvae centers of abundance in 2001 and 2002, and was associated with lower salinities and higher turbidities. Ichthyoplankton samples from this assemblage tended to be uniform in composition and almost exclusively contained striped bass yolk-sac and feeding-stage larvae and white perch feeding-stage larvae. Alosine and white perch yolk-sac larvae occurred further upbay and in lower turbidities in 2003 compared to feeding stages and all stages of striped bass (Figure 2-13).

Larval-Stage Abundance and Recruitment Potential

Concentrations of feeding-stage larvae varied considerably among the three years (Figure 2-14). Concentrations varied by more than three orders of magnitude for striped bass and more than one order of magnitude for white perch and alosines. Similarly, concentrations of age-0 juveniles (in July, approximately 60 days posthatch) exhibited high variability in these years and maintained their same rank order of abundance relative to larval stages. The link between larval and juvenile abundances

suggests that survival to the feeding larval stage in moronid and alosine taxa that generally were <30 days old was sufficient to coarsely describe relative strengths of age-0 year classes, at least in the three years studied.

Distributions of age-0 juveniles during summer in July were similar to spring larval distributions (Figure 2-15). In 2001, when freshwater flows were moderate, juvenile striped bass were distributed broadly throughout a 40-km segment, whereas white perch and alosine juveniles were most abundant further upbay above the salt front. Peak juvenile abundances of the three taxa during July 2001 occurred within 10km of the center of abundance of feeding-stage larvae in May. In contrast, under low-flow conditions in 2002, juveniles in July occurred over a narrow range and further upbay. Feeding-stage larvae during May 2002 were at low abundance and were distributed over a broad area. In 2003, when freshwater flows were highest, juvenile striped bass and white perch centers of abundance were 20km further downbay than in 2001 and 2002, and the juvenile alosine center of abundance was 10km further downbay than in 2002. Summer juvenile distributions appeared to be influenced by the spring distribution of feeding-stage larvae as well as the variable, among-years location of the ETM and salt front (Figure 2-6).

DISCUSSION

The spring ichthyoplankton assemblage in upper Chesapeake Bay exhibited conspicuous inter-annual variability in response to differing hydrological conditions and effects of those conditions on constituent taxa. Taxa that dominated assemblages

differed among years, e.g., alosines dominated in 2001 but moronids dominated in 2003; and, the low ichthyoplankton abundance in 2002 was characterized by common occurrence of cyprinid larvae. Turbidity, salinity, and depth explained a significant amount of the variability in distributions of individual larval taxa and overall assemblage structure. Salinity and turbidity define the location and strength of the salt front and ETM in the upper Bay nursery. Hydrological conditions and the degree that larvae are associated with the ETM and salt front play significant roles in determining recruitment success of anadromous fishes in the upper Bay. Annual differences in distributions of taxa relative to the ETM and salt front were modulated by freshwater flow levels, and larval distributions are related to larval abundances and apparent survival.

Hydrological Conditions and Abundances of Larval Taxa

Hydrological variability and larval association with the salt front and ETM probably affected survival and abundances of feeding-stage larvae. Concentrations of feeding-stage larvae were 13 times higher in 2003 than in 2002 when conditions were wet and dry, respectively. Striped bass and white perch were responsible for most of the increased abundance of larvae in 2003, comprising 84 percent of all feeding-stage fish larvae in this wet year. Hydrological conditions and the degree of association with the salt front may play significant roles in determining recruitment success of upper Bay anadromous fishes.

The highest pre-recruit abundances of juvenile striped bass and white perch in summer occurred in 2003 when the center of abundance of feeding-stage larvae was within the ETM, and when larval occurrences were lowest below the salt front and ETM. In contrast, poorest recruitments were registered in 2002 when there was no clear center of larval abundance and when larvae commonly occurred below the salt front. Yolk-sac and early feeding-stage striped bass and white perch larvae possibly suffered higher mortality in 2002 due to osmotic stress and advective down-estuary loss. Abundances of feeding-stage larvae for all anadromous taxa were correlated with relative levels of age-0 pre-recruit abundances two months later (Figure 2-14). Results reported here suggest that recruitment patterns are controlled, at least in part, by biophysical processes that enhance larval retention and increased spatial overlap with prey, and which are set up annually by variable spring, and possibly late-winter, weather patterns.

The findings support results from other research that evaluated the role of the ETM and salt front in larval fish retention and survival in Chesapeake Bay (North and Houde, 2001, 2003, 2006). For example, abundances and occurrences of feeding-stage larvae of striped bass and white perch differed in a wet (1998) and dry (1999) year (North and Houde, 2006). In 1999, larvae were uncommon and occurred in mean salinities of 2-5 compared to 1998 when larvae were abundant and occurred at mean salinities of 0-1. North and Houde proposed that moronid larvae at higher salinities face greater risk of mortality due to osmotic stress and down-estuary loss. Results of mark-recapture research on larval striped bass in the Patuxent River supported that proposal. There were virtually no recaptures of larvae released below the salt front,

indicating high mortality or advective losses from this zone (Secor et al., 1995). The high salinities of occurrence I observed in a dry year, 2002, the more dispersed distribution, and low apparent larval survival suggest that striped bass eggs and the yolk-sac larvae of all taxa were lost down-estuary or experienced high mortalities due to osmotic stress.

Positive associations between freshwater flow and recruitments of Chesapeake Bay striped bass, white perch, and alosines have been reported previously (Houde and Secor, 1996; McGovern and Olney, 1996; North and Houde, 2001; Wood, 2000; North and Houde, 2003). And, there was a positive relationship between flow and striped bass recruitment in the San Francisco Bay estuary (Turner and Chadwick, 1972; Kimmerer et al., 2001), although that relationship broke down in recent years. Positive relationships between flow and recruitment potential were reported for other anadromous or estuarine species in San Francisco Bay, e.g., American shad, longfin smelt *Spirinchus thaleichthys*, Pacific herring *Clupea pallasii*, starry flounder *Platichthys stellatus*, and Sacramento splittail *Pogonichthys macrolepidotus* (Kimmerer, 2002).

In some cases, freshwater flow may have negative effects or may not be important in controlling fish recruitment in estuaries (Rose, 1992). In the San Francisco Bay, effects of freshwater flow are positive for most fishes, although the Delta smelt *Hypomesus transpacificus* exhibited significant positive and negative relationship during 1988-1999 and 1972-1987 periods, respectively (Kimmerer, 2002). In the Hudson River, moronid recruitments apparently are less responsive to temperature and freshwater flow than in Chesapeake Bay, and it has been suggested

that the large volume of nursery habitat in the Hudson dampens physical variability (Limburg et al., 1999). Research on fish larvae in the Chikugo River ETM demonstrated that the ETM exerts a strong control over distribution of the calanoid copepod *Sinocalanus sinensis*, the dominant prey of larval fishes in the oligohaline region of this tidal river (Islam and Tanaka, 2007). *Sinocalanus* abundance is negatively influenced by freshwater flow. Furthermore, recruitment of Japanese seaperch *Lateolabrax japonicus* recruitment in upper Ariake Bay and the Chikugo River estuary was not related to freshwater flow (Shoji et al., 2006), although the authors suggested that negative and positive effects of flow on *Lateolabrax* recruitments were possible. In the Connecticut River, recruitment levels of American shad were negatively correlated with freshwater discharge (Crecco and Savoy, 1984).

The positive effect of freshwater flow or recruitment of fishes in coastal plain estuaries like Chesapeake Bay probably differs from effects in other estuaries because dominant ichthyofauna, including alosines and moronids, occur near the salt front and ETM in Chesapeake Bay where retention may reduce risk of down-estuary loss. This is especially probable under conditions of high freshwater flow that enhance gravitational circulation (Hetland and Geyer, 2004).

Spatial Patterns in Larval Distribution

There are species-specific and stage-specific differences in transport to, and utilization of, the ETM region. Striped bass yolk-sac stages were generally associated with the location of the ETM in 2001 and 2003 when freshwater flows were average

and high, respectively. Feeding-stages of striped bass were more strongly associated with the ETM and salt front location, especially in the wet year 2003. White perch larvae were not associated with the ETM until the feeding stage. These findings are consistent with earlier research (North and Houde, 2001, 2003), and corroborate the suggestion that striped bass eggs and white perch yolk-sac larvae are transported to the ETM and salt front where feeding-stage larvae are retained.

Alosine and white perch larvae are transported to the ETM during the yolk-sac stage. White perch eggs are demersal, adhering to the substrate, and are not subject to transport. However, eggs of the alosines, blueback herring and alewife, at spawning have adhesive and demersal properties but then disperse into the water column and drift after water hardening. Distributions of alosine yolk-sac and feeding-stage larvae suggest that transport occurs during the yolk-sac stage because only larvae in the feeding stage are associated with the ETM. A coupled biological-physical model indicated that striped bass eggs in the upper Bay can be transported to the ETM within 2 days (North et al., 2005), which is approximately the duration of the egg stage. Egg-stage duration does not explain patterns in alosine transport and retention because alewife and blueback herring eggs require >4 days to hatch at temperatures observed during my study (Cianci, 1969; Morgan and Prince, 1976).

Differences in spawning location of striped bass and alosines may explain taxa-specific differences in down-estuary transport to the ETM. Blueback herring and alewife generally spawn further up-estuary in tidal freshwaters, or upriver of tidal influences, whereas striped bass spawns within and just above the salt front. Consequently, most striped bass larvae probably hatch at about the time they are

transported to the ETM, while alosines hatch before reaching the ETM and cannot be associated with the ETM until the older feeding larval stage.

Sampling depth was a significant variable explaining abundances of dominant taxa in the GAMs and Assemblage Structure analyses. The significant effects of depth on larval occurrences and concentrations highlight the importance of evaluating vertical distributions of larvae in estuaries despite their typically shallow depths. Strong vertical gradients in hydrographic variables are common in all but the most well-mixed estuaries or during drought years when residual circulation is reduced or non-existent (Bennett et al., 2002). Failure to determine vertical distributions of larvae can obscure taxa-environmental relationships and also interpretation of assemblage structure. For example, species overlaps and potential competitive interactions may appear strong, lacking evaluation of how species segregate by depth.

Transport to, retention within, and loss from estuarine nurseries can be controlled by vertical distributions of fish larvae. Vertical migration behaviors promoting retention are common and species-specific depth associations have implications for annual differences in survival and assemblage structure ((Norcross and Shaw, 1984; Boehlert and Mundy, 1988; Rowe and Epifanio, 1994; Bailey and Picquelle, 2002; Bennett et al., 2002).. Species that locate at mid and near-bottom depths at the salt front and ETM can minimize or avoid down-estuary loss. Other species may use selective tidal stream transport to maintain their location by only migrating toward surface on flood tides (Boehlert and Mundy, 1988). In the upper Chesapeake Bay, the observed association of moronid larvae with deeper layers of the

water column almost certainly is effective in promoting retention above and within the salt front, and this behavior may have been selected to increase recruitment potential.

My results clearly indicated a positive affinity for bottom and mid depths by moronid larvae. In 1998 and 1999, North and Houde (2006) also reported highest concentrations of moronid larvae deep in the water column in the upper Bay ETM and salt front. They suggested that larvae were tracking zooplankton prey, primarily the copepod *Eurytemora affinis*, which tended to be most abundant at depth, and consequently the moronid larvae promoted their own retention. A contrasting situation may operate in San Francisco Bay where striped bass, yellowfin goby (*Acanthobobius flavimanus*), and longfin smelt (*Spirinchus thaleichthys*) make tidally-timed or reverse-diel vertical migrations (Bennett et al., 2002). Such differences in vertical migration behaviors in different systems led North and Houde (2006) to propose that tracking prey with differing depth distributions or migratory behavior might be one common explanation for differences in vertical migration behaviors among fish larvae.

Vertical-orientation behaviors that promote retention may be especially important during years when freshwater flows is reduced and estuarine gravitational circulation is minimized or non-existent (Bennett et al., 2002). In low freshwater flow years, striped bass and white perch larvae at mid and bottom depths would be at an advantage compared to alosines that are associated with surface waters. During moderate and high freshwater flow years residual circulation will be up-estuary at all depths below a threshold that may be defined by the 1.0 isohaline. Thus, in high flow years simply avoiding surface water may be adequate to avoid down-estuary loss.

However, when freshwater flows are reduced more complex behaviors such as selective tidal-stream transport may be necessary. Plasticity in behavior was demonstrated in the San Francisco estuary where striped bass and longfin smelt, *Spirinchus thaleichthys*, vertically migrated on a tidal basis during a drought year but migrated on a reverse diel cycle during a year with higher freshwater flows (Bennett et al., 2002). I did not detect selective tidal-stream transport by moronid larvae during the dry year in my study, although a more careful evaluation of vertical distribution patterns across tidal cycles would be necessary to rule it out.

The vertical distribution of alosine larvae indicated surface and mid-depth affinities. To my knowledge, no reports on vertical distribution patterns of larval American shad, blueback herring and alewife, or other alosines are available because published research reported results from oblique net tows without depth-specific sampling (Bilkovic et al., 2002; Campfield, 2005; Walsh, 2005). Alosine larvae in surface waters near the salt front and ETM must be more vulnerable to advective loss. In my observations, distribution of alosines extended further downbay to well below the salt front compared to striped bass and white perch larvae in 2002 when recruitment was poor for all taxa. Alosines may not be able to migrate or maintain position at deeper depths, or they may select shallow depths as a tradeoff for other advantages such as higher light level (Shoji et al., 2005; North and Houde, 2006), lower turbidity and higher transparency, in addition to warmer temperatures, lower salinities, and higher dissolved oxygen levels. Such tradeoffs, operating to counter risk of advective loss, could enhance feeding success, growth, and survival of larvae.

Environmental Determinants of Assemblage Structure

Broad-scale distribution patterns reported here are thought to be primarily determined by abiotic factors. Similar conclusions were reached in other research on larval fish assemblages (Sabates, 1990; Smith et al., 1999; Campfield, 2005). These results and interpretation are consistent with theory in community ecology in which large-scale patterns in distributions of organisms are believed to be explained best by abiotic factors while smaller-scale patterns are determined by biological interactions (Menge and Olson, 1990).

Spatial variation was positively related to the level of annual spring freshwater discharge. Results of the CCA explained a higher proportion of assemblage variability in wet (0.30) and moderate (0.27) discharge years than in the dry year (0.20). My findings are consistent with results from an ichthyoplankton assemblage analysis on the Patuxent River in which assemblages were more structured along abiotic gradients when flow was high (Campfield, 2005). In my research, downbay distance, salinity, and depth were most important in explaining ichthyoplankton distribution and assemblage structure. Two of these variables, downbay distance and salinity, are directly dependent on inter-annual hydrological variability, highlighting the importance of annual freshwater discharge levels in shaping the upper Bay ichthyoplankton assemblage. Another important abiotic determinant of assemblage structure was turbidity, which had both positive and negative relationships with distributions of moronids and alosine larvae, respectively.

In the GAMs analysis, salinity was a significant variable in at least one of the years for each of the taxa considered (Figure 2-7). The relationship between salinity and larval abundance was either negative or positive and varied among taxa and years. In general, larvae of most taxa were associated with low salinities and freshwater during 2001 and 2003 when freshwater discharge levels were moderate and high, respectively, and fish larvae occurred in higher salinities during 2002, the dry year. Most taxa had peak larval abundances near the salt front during at least one year. High moronid concentrations were rare below the salt front in any year, whereas alosine larvae were abundant below the salt front in the dry year, 2002. In my study, concentrations of moronids and alosines were usually highest up-estuary and within the salt front relative to locations down-estuary.

In other estuaries, salinity is an important factor controlling ichthyoplankton assemblages and distributions. For example, concentrations of estuarine fish larvae within the St. Lucia estuary, South Africa, were negatively correlated with salinity (Harris et al., 1999). Similarly, dominant estuarine species in the Tanshui River Estuary, Taiwan, exhibited a negative relationship with salinity (Tzeng and Wang, 1993). The authors suggested that salinity acts as a cue for migrations by late-stage larvae to inshore nursery grounds.

In the dry year 2002, when apparent larval survival was low striped bass yolk-sac and white perch yolk-sac and feeding-stage larvae were positively associated with moderate turbidities. Alosines exhibited a negative association with turbidity in the wet year 2003, apparently a result of their near-surface distribution at locations where turbidities were relatively low in the upper Bay. The moronid association with high

turbidities in 2002 agrees with other reports on larval moronids in the upper Bay ETM. For example, larval striped bass and white perch were found at both higher salinities and higher turbidities in a dry (1999) compared to a wet (1998) year (North and Houde, 2003, 2006). My research revealed that moronids in 2003 were strongly associated with the ETM, but not necessarily associated with highest turbidities in the ETM center. In 2003, moronid larvae concentrations were highest at the up-estuary boundary of the ETM, just up-estuary of the maximum turbidities and in freshwater or very low salinity. My interpretation of the observed patterns and also the interpretation by North and Houde (2001) is that some larvae are retained in the ETM in dry years, but that the ETM is located in higher salinities in response to the up-estuary displacement of the salt front. Retention in the ETM during dry years could have negative consequences if larvae are retained where osmotic stress and risk for down-estuary loss are high.

Turbidity generally is considered to be an important determinant of larval and juvenile fish assemblages in estuaries. For example, turbidity and salinity alone accounted for 45% of the variation in ichthyoplankton assemblages in the St. Lucia Estuary, South Africa (Harris et al., 1999). Research evaluating the role of ETMs for larval fish survival in the Chesapeake Bay (North and Houde, 2001, 2003) and the St. Lawrence River estuary, Canada (Sirois and Dodson, 2000), pointed to possible advantages of high turbidities in enhancing foraging success, serving as predation refuge (Chesney, 1989), as well as lowering metabolic costs due to decreased swimming activity when turbidity is high and prey resources are sufficient (Sirois and Dodson, 2000).

Temperature did not explain much of the variability in assemblage structure of larval fishes in upper Chesapeake Bay. The lack of a strong effect, while somewhat surprising, probably resulted because of the short temporal period in which research cruises were conducted each year. The collections and analysis, in effect, held season constant because the cruises were conducted exclusively during May. This design was sufficient to analyze inter-annual and spatial variability in ichthyoplankton, but could not follow seasonal trends or effects of fluctuating temperatures. Other ichthyoplankton surveys that were conducted over a broader seasonal period commonly have reported strong temperature effects on coastal ichthyoplankton assemblages; e.g., from Chesapeake Bay (Campfield, 2005), the Gulf of Tonkin (Belyanina, 1986), the Tanshui River estuary, Taiwan (Tzeng and Wang, 1993), and the St. Lucia estuary, South Africa (Harris et al., 1999).

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Table 2-1. Cruise dates, Tucker trawl sampling effort, mean concentration of all collected yolk-sac and feeding-stage fish larvae (no. m⁻³) included in this study, and standard deviation (sd) for May 2001, May 2002, and May 2003 surveys.

	Number of Tows	Feeding-Stage Larvae	sd	Yolk-sac Larvae	sd
May 7-15 2001	130	8.85	12.63	3.89	4.44
May 6-14 2002	126	1.28	2.32	3.08	4.44
May 13-15 2003	65	16.71	20.31	8.25	8.55

Table 2-2. Cruise dates, mean and standard deviation (sd) for temperatures (° C), salinities, dissolved oxygen (mg/ l), and turbidities averaged over surface to bottom in May 2001, May 2002, and May 2003 surveys.

	Temperature	sd	Salinity	sd	Oxygen	sd
May 7-15 2001	18.96	1.64	1.78	2.64	6.69	0.91
May 6-14 2002	17.37	1.13	2.12	2.96	8.15	1.70
May 13-15 2003	16.46	1.31	2.46	3.71	7.63	1.3

Table 2-3. Lambda scores for the first four canonical correspondence analysis (CCA) axes and cumulative percentage of variation explained for CCA on 2001, 2002, and 2003 ichthyoplankton. Lambda, or eigenvalues, are the amount of total variance explained by each axis.

Partitioning of mean squared contingency coefficient:				
Total	1.34			
Constrained	0.40			
Unconstrained	0.94			
Eigenvalues, and their contribution to the mean squared contingency coefficient				
	CCA1	CCA2	CCA3	CCA4
lambda	0.21	0.13	0.05	0.01
variance	0.16	0.25	0.29	0.30

Table 2-4. Results from generalized additive model (GAM) analysis on effect of selected environmental variables on the distribution of yolk-sac and feeding stages of dominant ichthyoplankton in upper Chesapeake Bay. Bold values in table are p values for variables selected in the final model. Variables without p values were not considered important for that taxon and year. Depth consisted of three different levels and selection was based on different criteria (see text), 'Y' indicates depth was important. ns=not selected.

Taxon	Year	Final Model AIC	Downbay Distance	Salinity	Temperature	Turbidity	Oxygen	Depth
Striped Bass								
Feeding Stage	2001	-476	0.0006	ns	ns	ns	ns	Y
	2002	-959	0.006	0.33	ns	ns	ns	
	2003	441	0.21	0.22	ns	ns	ns	Y
Yolk sac	2001	-280	0.0007	ns	ns	ns	ns	Y
	2002	-388	0.15	0.0004	ns	0.03	ns	
	2003	246	0.004	ns	ns	ns	ns	Y
White Perch								
Feeding Stage	2001	646	ns	<0.0001	ns	ns	ns	Y
	2002	515	ns	0.002	ns	<0.0001	.0.0002	
	2003	523	0.31	0.36	ns	ns	ns	Y
Yolk sac	2001	476	<0.0001	ns	ns	ns	ns	Y
	2002	684	ns	ns	ns	<0.0001	0.04	
	2003	260	0.27	ns	ns	ns	0.0002	
Alosines								
Feeding Stage	2001	977	ns	0.0007	ns	ns	ns	Y
	2002	126	ns	ns	ns	ns	0.25	
	2003	302	ns	ns	0.19	ns	ns	
Yolk sac	2001	642	0.0008	0.13	ns	ns	ns	Y
	2002	258	0.03	ns	ns	ns	0.49	Y
	2003	329	<0.0001	0.002	ns	<0.0001	ns	Y
Cyprinidae								
Feeding Stage	2001	-1046	ns	0.48	ns	ns	Ns	
	2002	-644	0.31	ns	ns	ns	Ns	
	2003	-473	Ns	ns	ns	ns	0.03	

Table 2-5. Lambda scores for the first four canonical correspondence analysis (CCA) axes and cumulative percentage of variation explained for CCA on 2001 ichthyoplankton. Lambda, or eigenvalues, are the amount of total variance explained by each axis.

Partitioning of mean squared contingency coefficient:

Total 0.79
 Constrained 0.24
 Unconstrained 0.55

Eigenvalues, and their contribution to the mean squared contingency coefficient

	CCA1	CCA2	CCA3	CCA4
lambda	0.14	0.07	0.02	0.01
variance	0.18	0.27	0.29	0.31

Table 2-6. Lambda scores for the first four canonical correspondence analysis (CCA) axes and cumulative percentage of variation explained for CCA on 2002 ichthyoplankton. Lambda, or eigenvalues, are the amount of total variance explained by each axis.

Partitioning of mean squared contingency coefficient:

Total 0.93
 Constrained 0.20
 Unconstrained 0.74

Eigenvalues, and their contribution to the mean squared contingency coefficient

	CCA1	CCA2	CCA3	CCA4
lambda	0.15	0.04	0.01	0
variance	0.16	0.20	0.21	0.21

Table 2-7. Lambda scores for the first four canonical correspondence analysis (CCA) axes and cumulative percentage of variation explained for CCA on 2003 ichthyoplankton. Lambda, or eigenvalues, are the amount of total variance explained by each axis.

Partitioning of mean squared contingency coefficient:

Total 0.63
 Constrained 0.21
 Unconstrained 0.42

Eigenvalues, and their contribution to the mean squared contingency coefficient

	CCA1	CCA2	CCA3	CCA4
lambda	0.16	0.03	0.01	0.01
variance	0.25	0.30	0.31	0.33

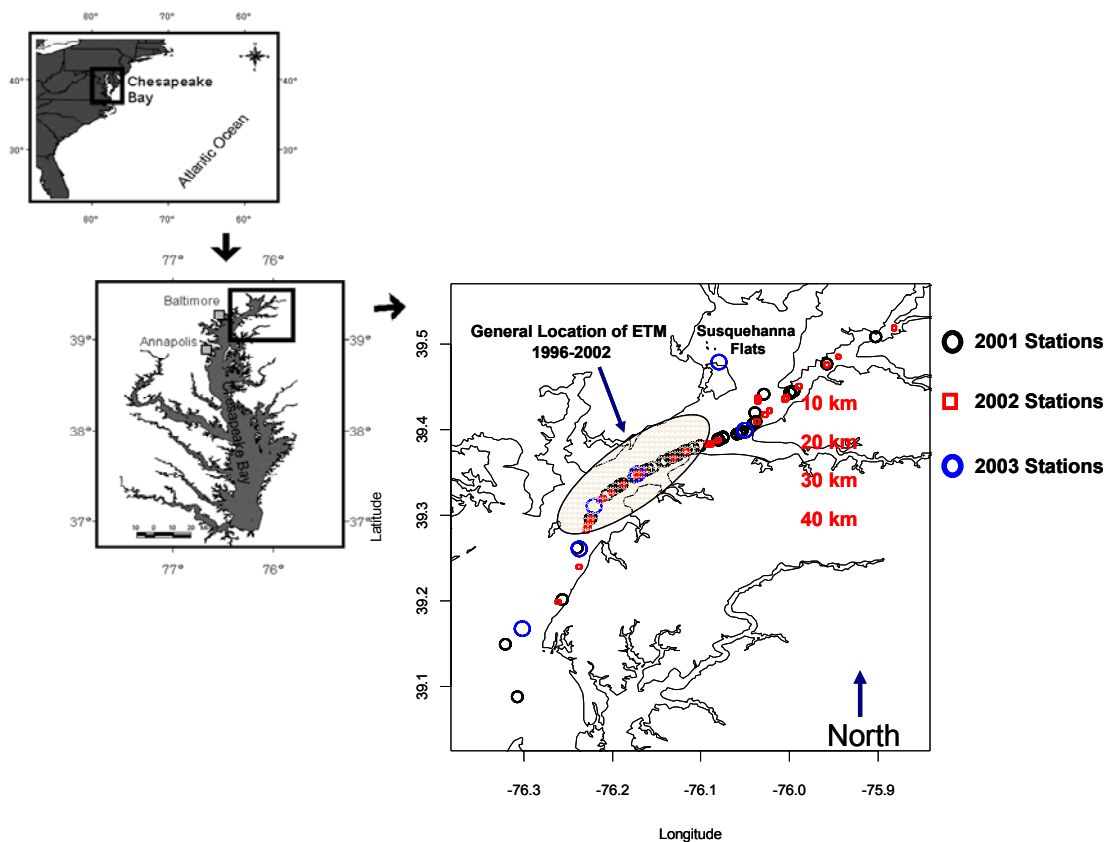


Figure 2-1. Research location and sampling stations in upper Chesapeake Bay during May 2001-2003. Distances (km) downbay from the Susquehanna River mouth are indicated on the right side of the map.

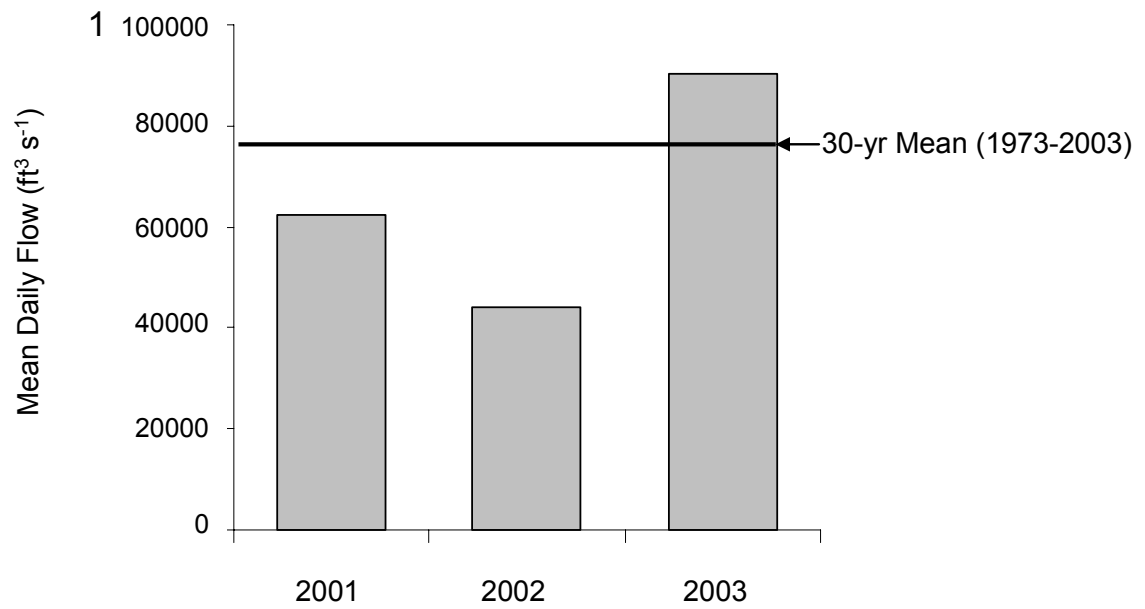


Figure 2-2. Mean daily Susquehanna River discharge (flow) during March and April at USGS Conowingo Dam station in the three years of this research.

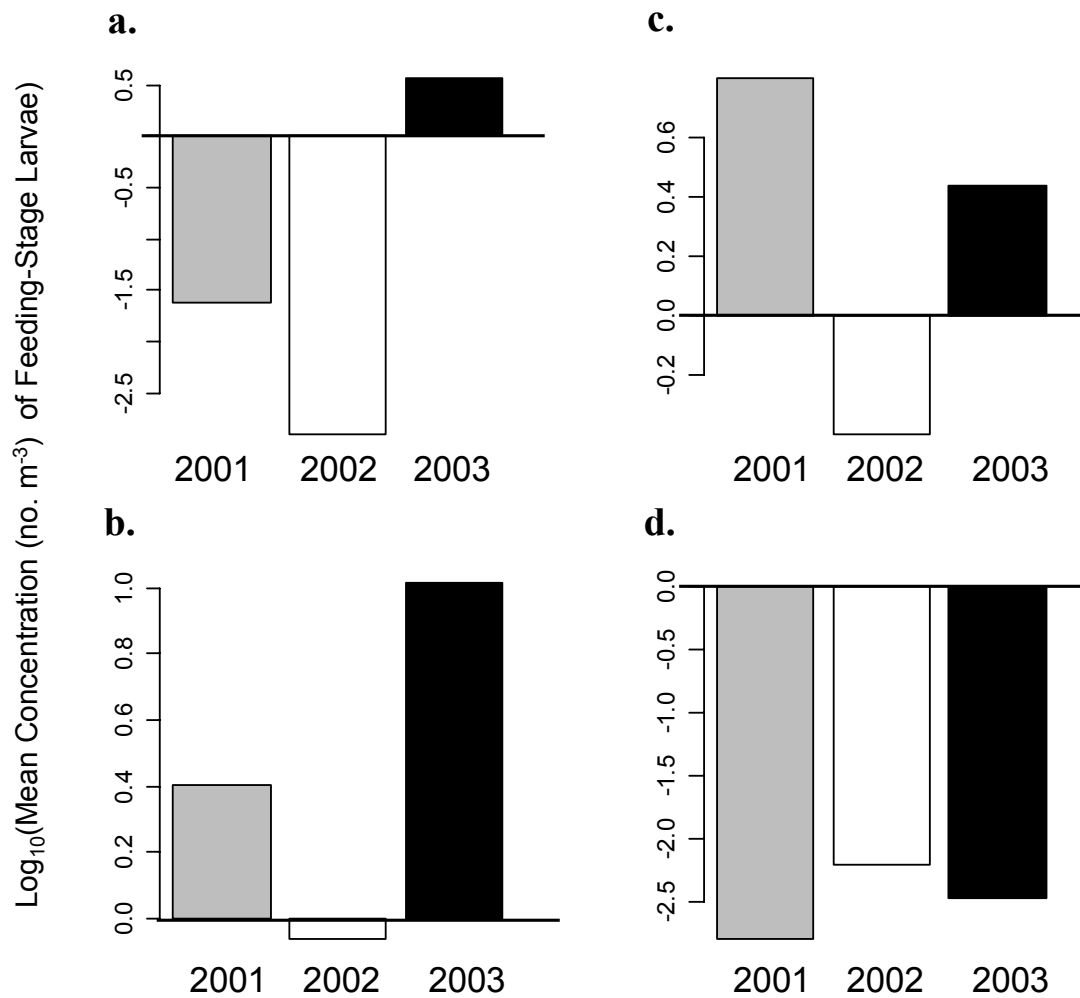


Figure 2-3. Concentrations of feeding-stage a) striped bass, b) white perch, c) alosines, and d) Cyprinidae in upper Chesapeake Bay during May 2001, 2002, and 2003. Values are on a log-scale; thus, mean concentrations below 1 individual per m^{-3} appear as negative values on plots.

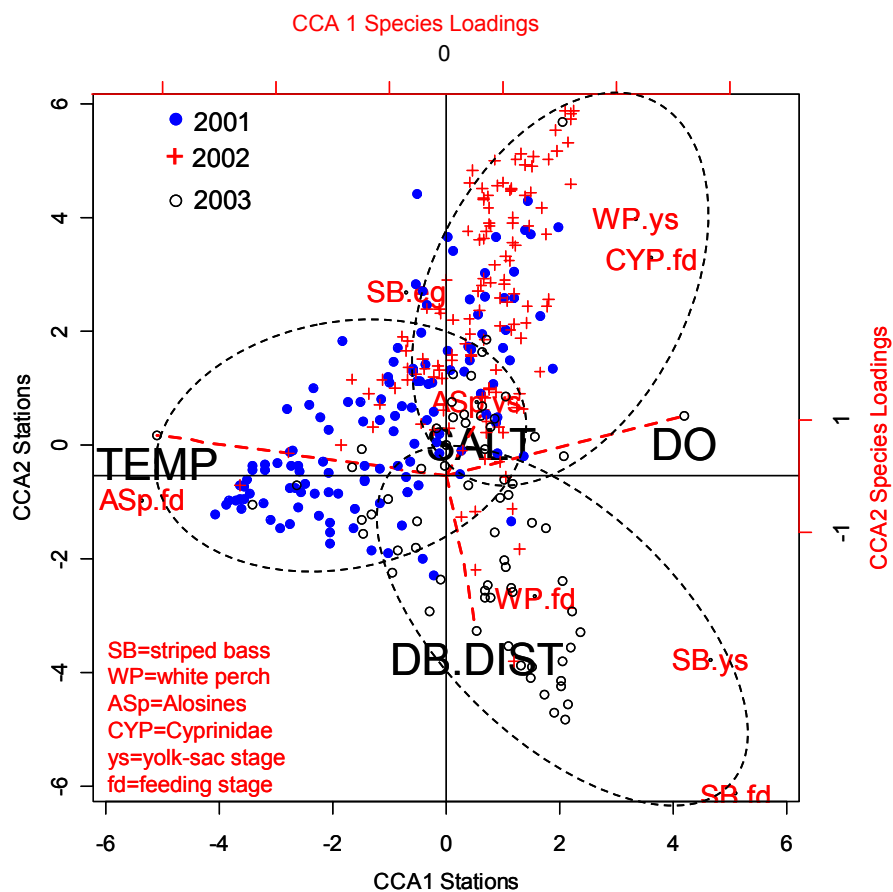


Figure 2-4. Canonical correspondence analysis (CCA) of BITMAX ichthyoplankton collections and environmental data during May 2001, 2002, and 2003.

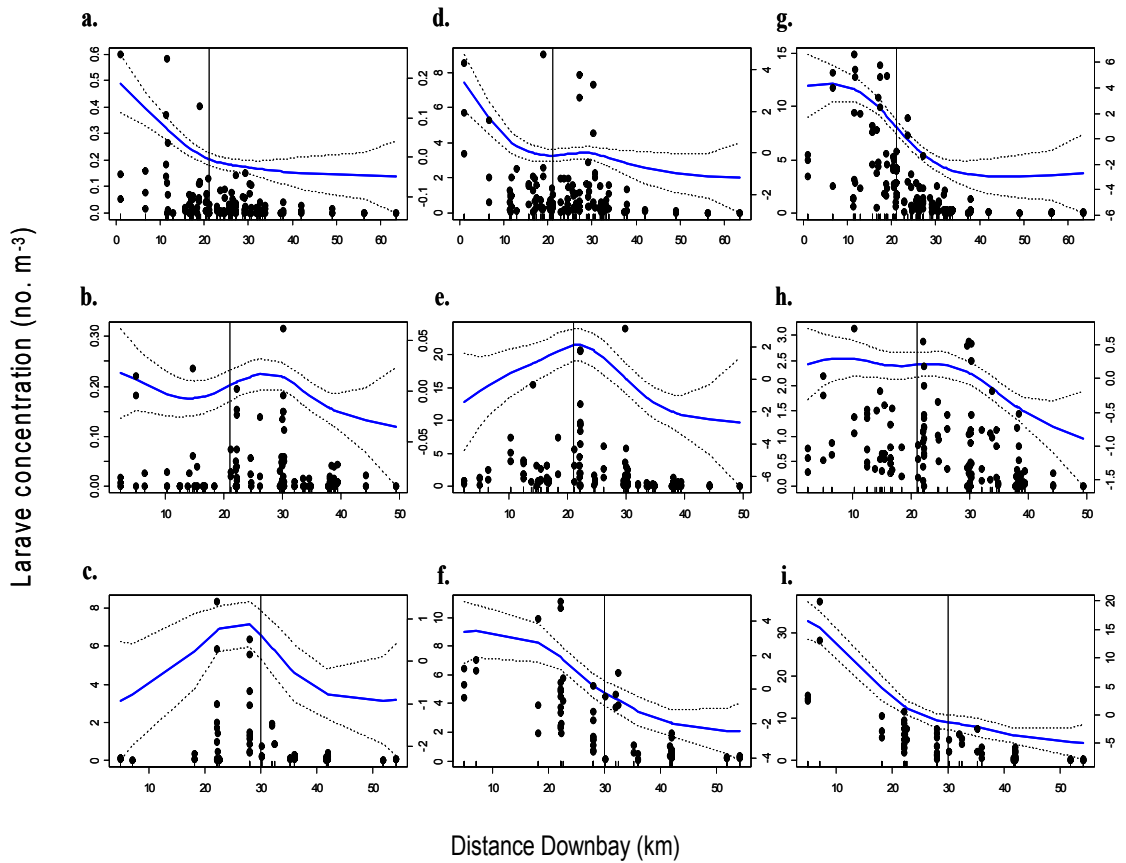


Figure 2-5. Distribution of striped bass (a - c), white perch (d - f), and alosine (g - i) yolk-sac larvae in upper Chesapeake Bay during May 2001, 2002, and 2003 with years shown in order from top to bottom of page. Observed (left axis) and generalized additive model (GAM) smooth fits (right axis) of larvae concentrations (no. m⁻³) against distance downbay (km) from the Susquehanna River mouth are shown. The solid line represents the conditional effect (negative and positive values) on mean larval concentration and the dashed lines represent the 95% confidence interval. Vertical line indicates the median location of maximum turbidity in each year. Note different scales on y-axes.

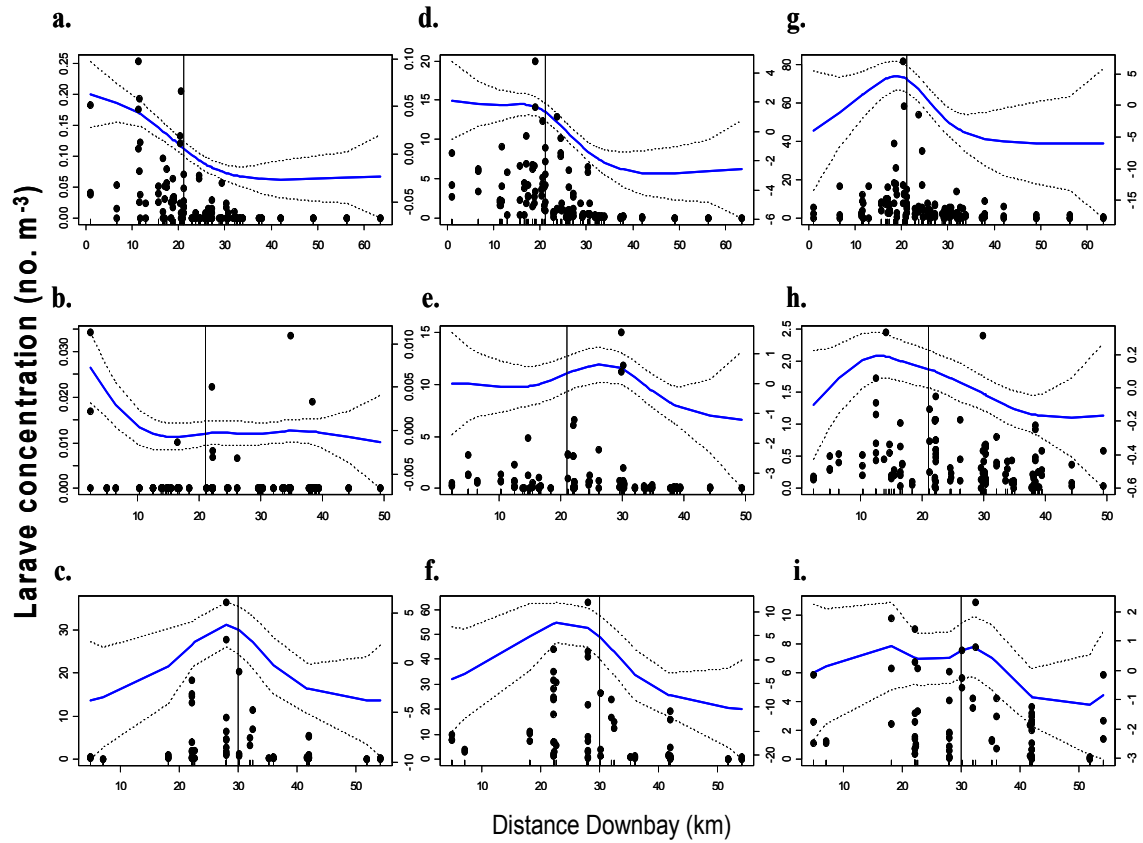


Figure 2-6. Distribution of striped bass (a - c), white perch (d - f), and alosine (g - i) feeding-stage larvae in upper Chesapeake Bay during May 2001, 2002, and 2003 with years shown in order from top to bottom of page. Observed (left axis) and generalized additive model (GAM) smooth fits (right axis) of larvae concentrations (no. m⁻³) against distance downbay (km) from the Susquehanna River mouth are shown. The solid line represents the conditional effect (negative and positive values) on mean larval concentration and the dashed lines represent the 95% confidence interval. Vertical line indicates the median location of maximum turbidity in each year. Note different scales on y-axes.

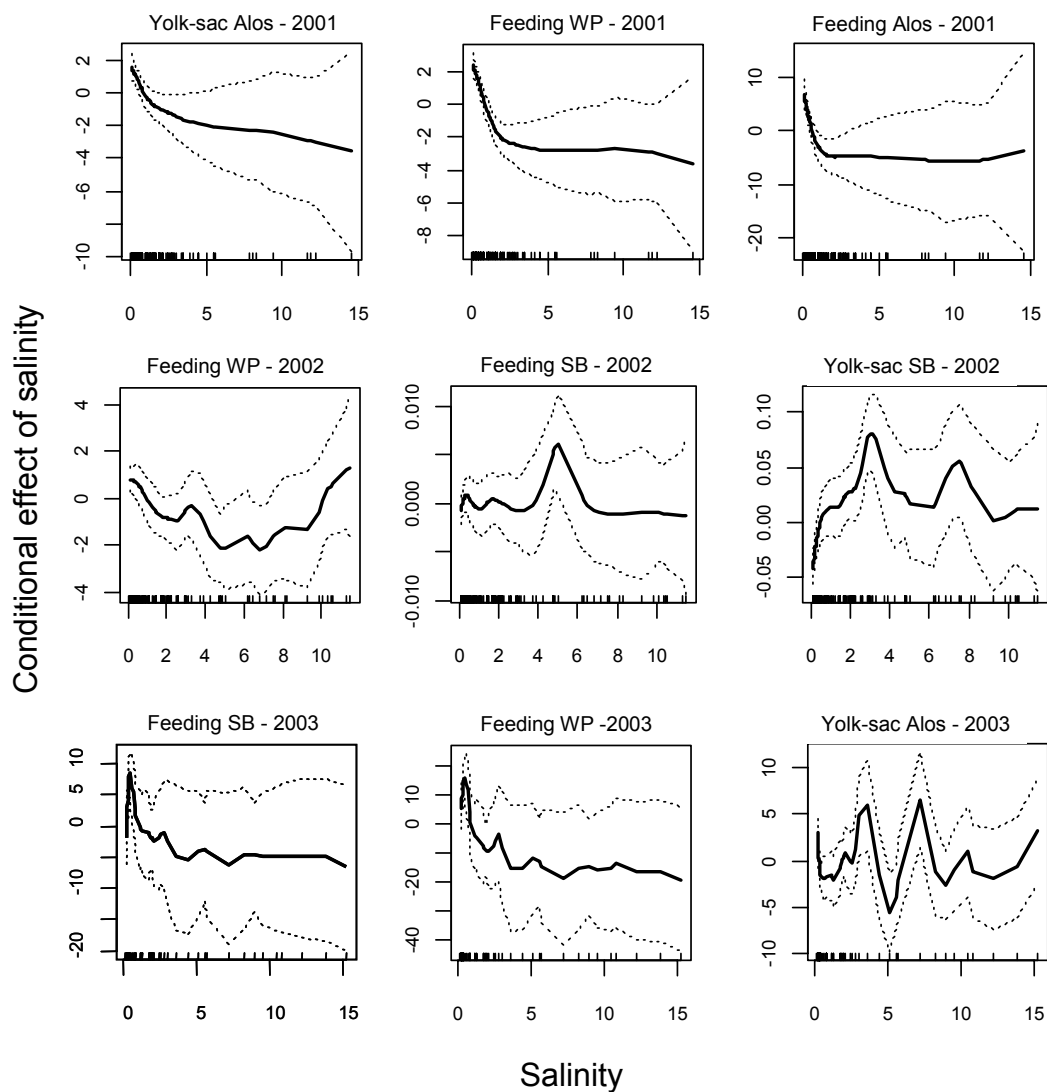


Figure 2-7. Salinity effects on the distribution of ichthyoplankton in upper Chesapeake Bay. Salinity was selected as an important determinant in a generalized additive model (GAM) predicting the concentration (no. m^{-3}) of larvae for taxa and years shown. The x-axis represents salinity and the y-axis represents partial residuals, or conditional effects, of salinity on the concentration of larvae. SB=striped bass, WP=white perch, Alos=Alosine.

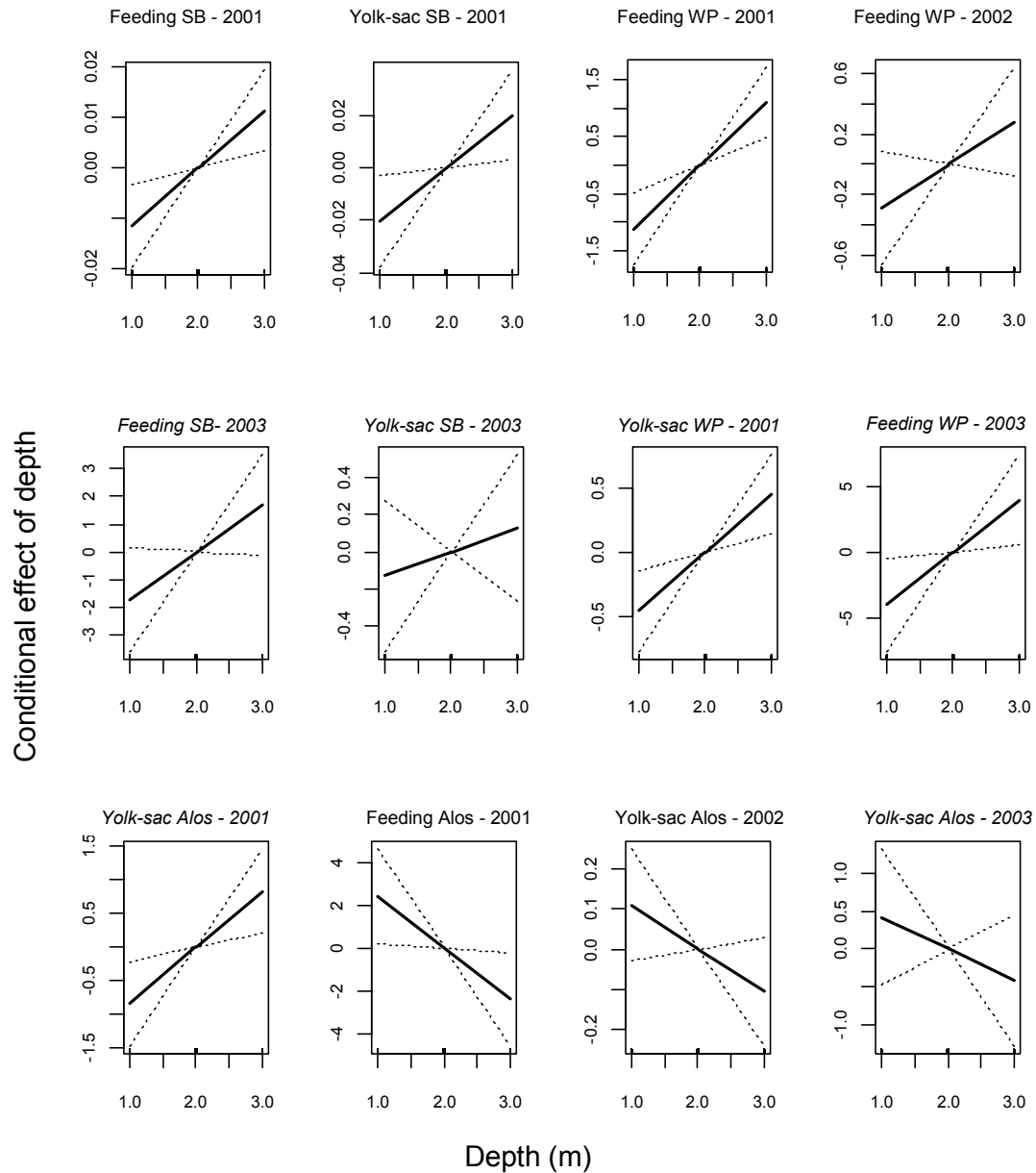


Figure 2-8. Depth effects on the distribution of ichthyoplankton in upper Chesapeake Bay. Depth was selected as an important determinant in a generalized additive model (GAM) predicting the concentration (no. m^{-3}) of larvae for taxa and years shown. The x-axis represents depth (1=surface, 2=mid depth, 3=bottom) and the y-axis represents partial residuals, or conditional effects, of depth on the concentration of larvae. SB=striped bass, WP=white perch, Alos=Alosine.

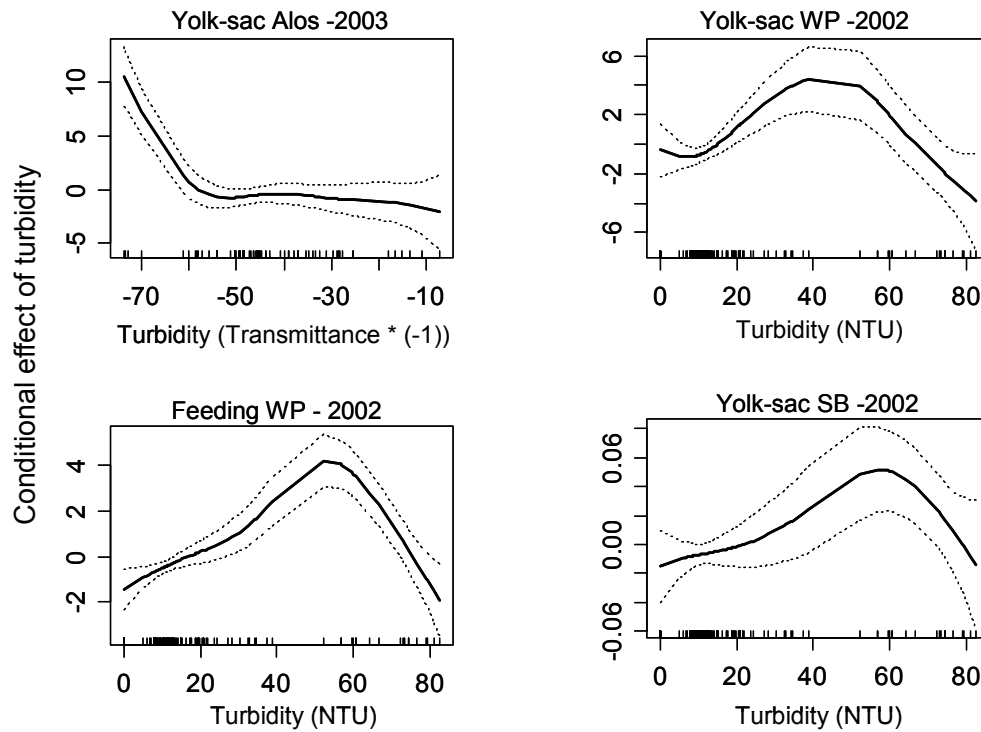


Figure 2-9. Turbidity effects on the distribution of ichthyoplankton in upper Chesapeake Bay. Turbidity was selected as an important determinant in a generalized additive model (GAM) predicting the concentration (no. m^{-3}) of larvae for taxa and years shown. The x-axis represents turbidity and the y-axis represents partial residuals, or conditional effects, of turbidity on the concentration of larvae. SB=striped bass, WP=white perch, Alos=Alosine.

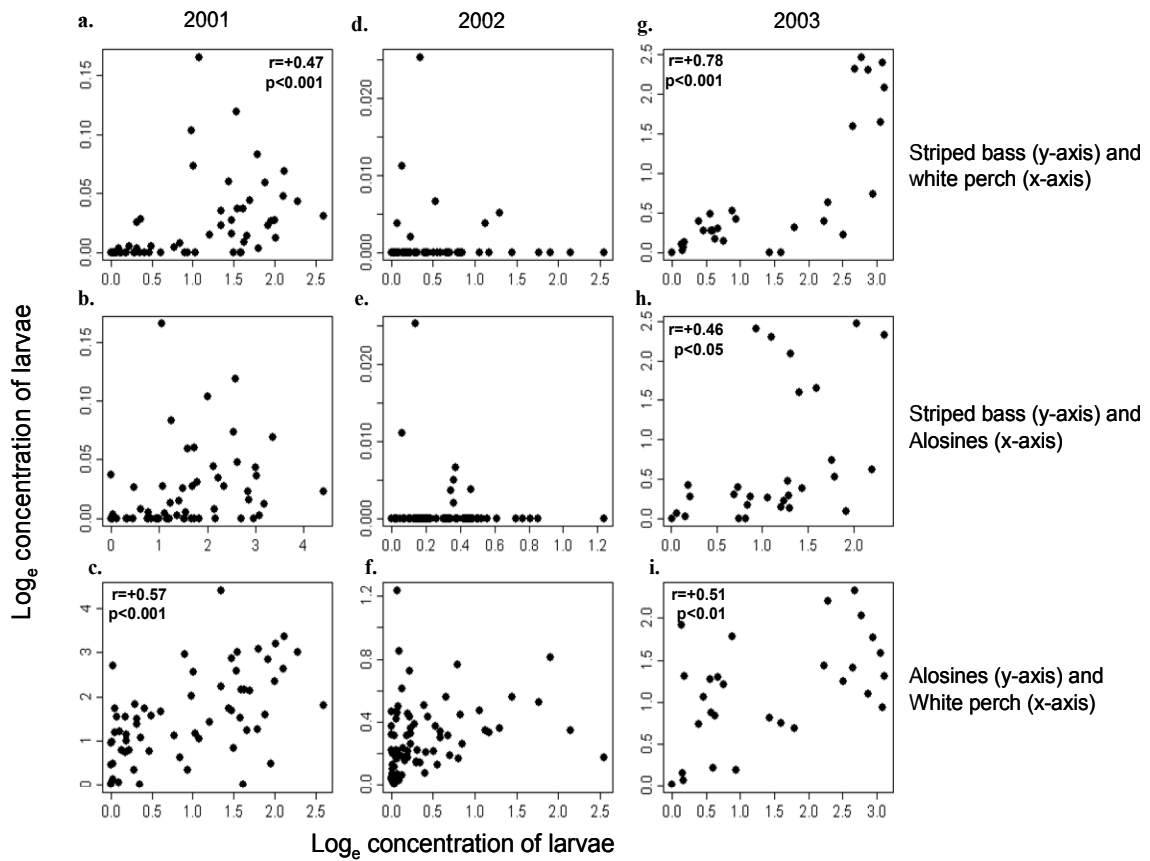


Figure 2-10. Pairwise correlations between the concentration of feeding stages of major ichthyoplankton taxa in the upper Chesapeake Bay in 2001, 2002, and 2003. Plots in top row are for striped bass versus white perch, second row down is striped bass versus alosine species, and the bottom plot is alosine species versus white perch. Correlation statistics are shown for relationships that were significant at $p<0.01$ and $r^2 \geq .10$.

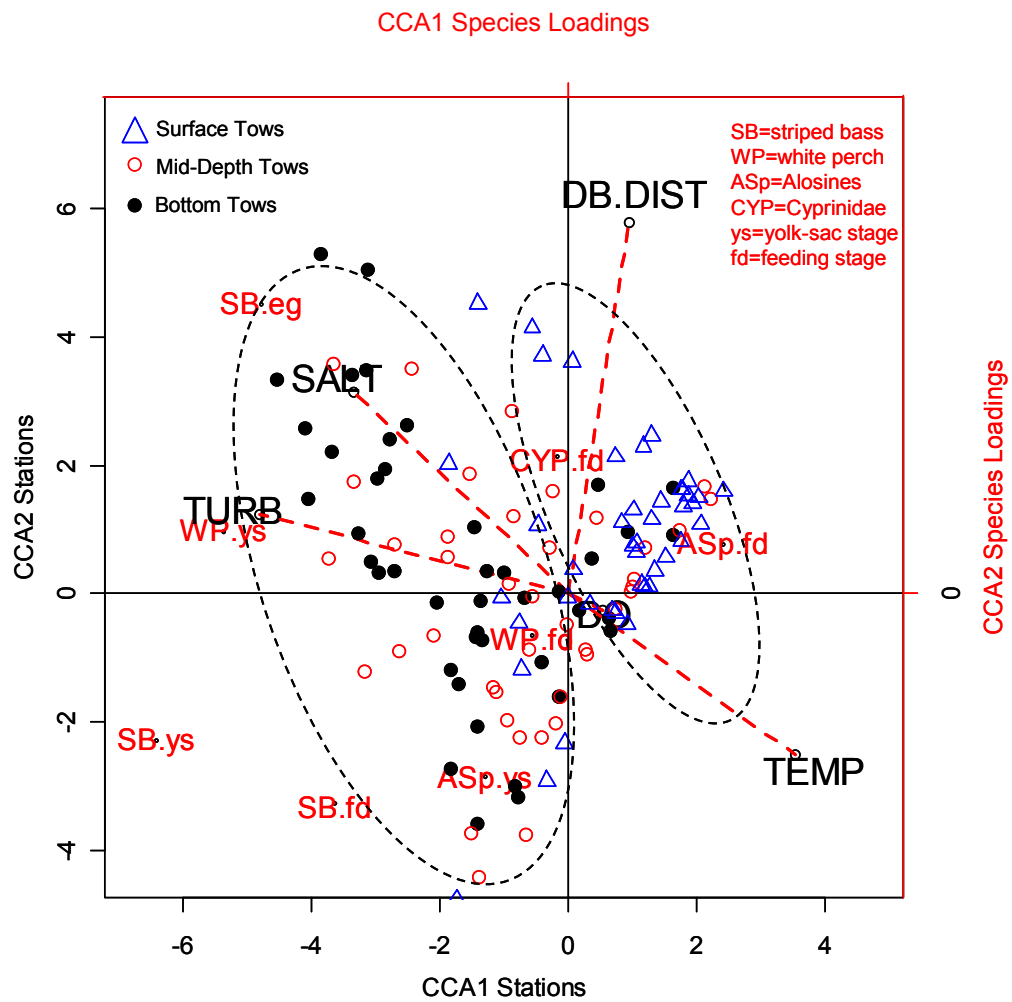


Figure 2-11. Canonical correspondence analysis of BITMAX ichthyoplankton collections and environmental data in May 2001.

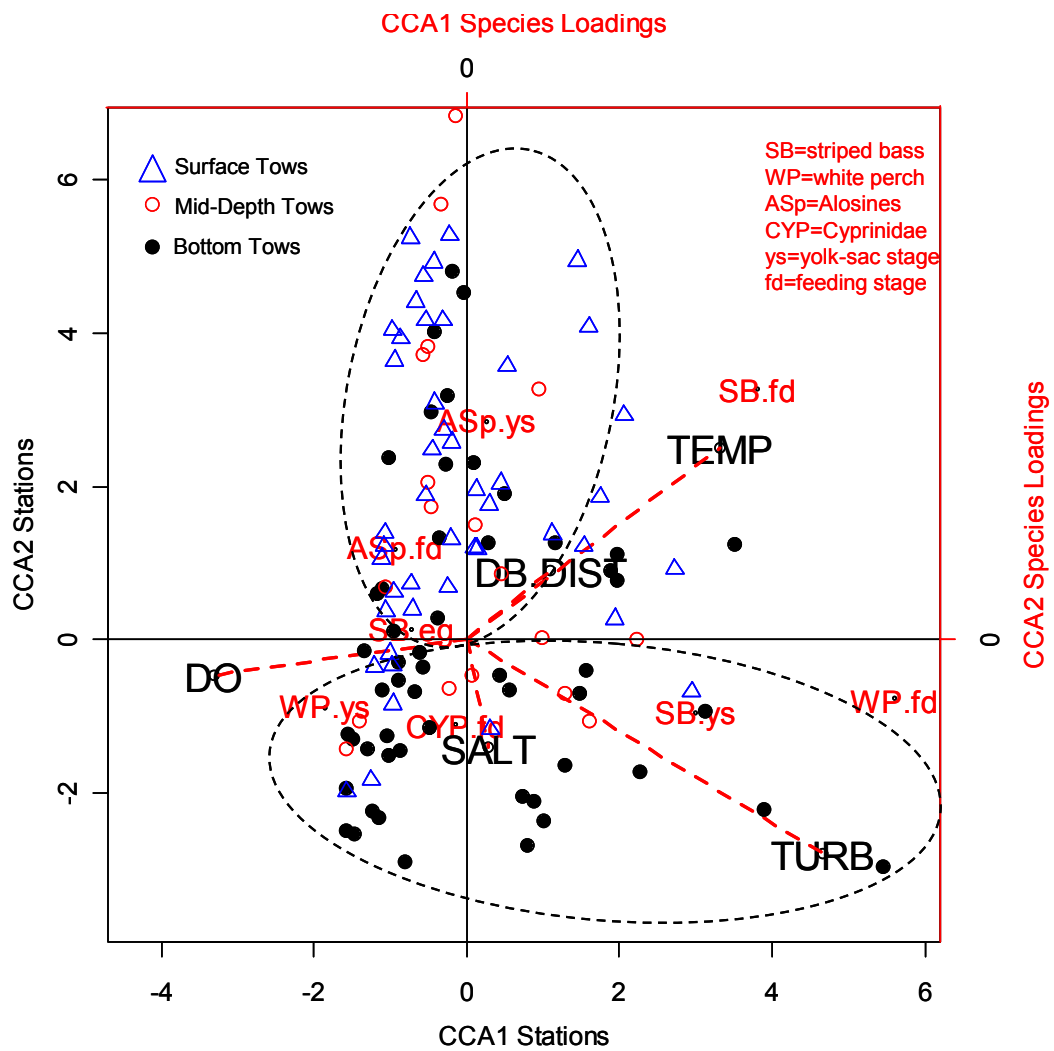


Figure 2-12. Canonical correspondence analysis of BITMAX ichthyoplankton collections and environmental data in May 2002.

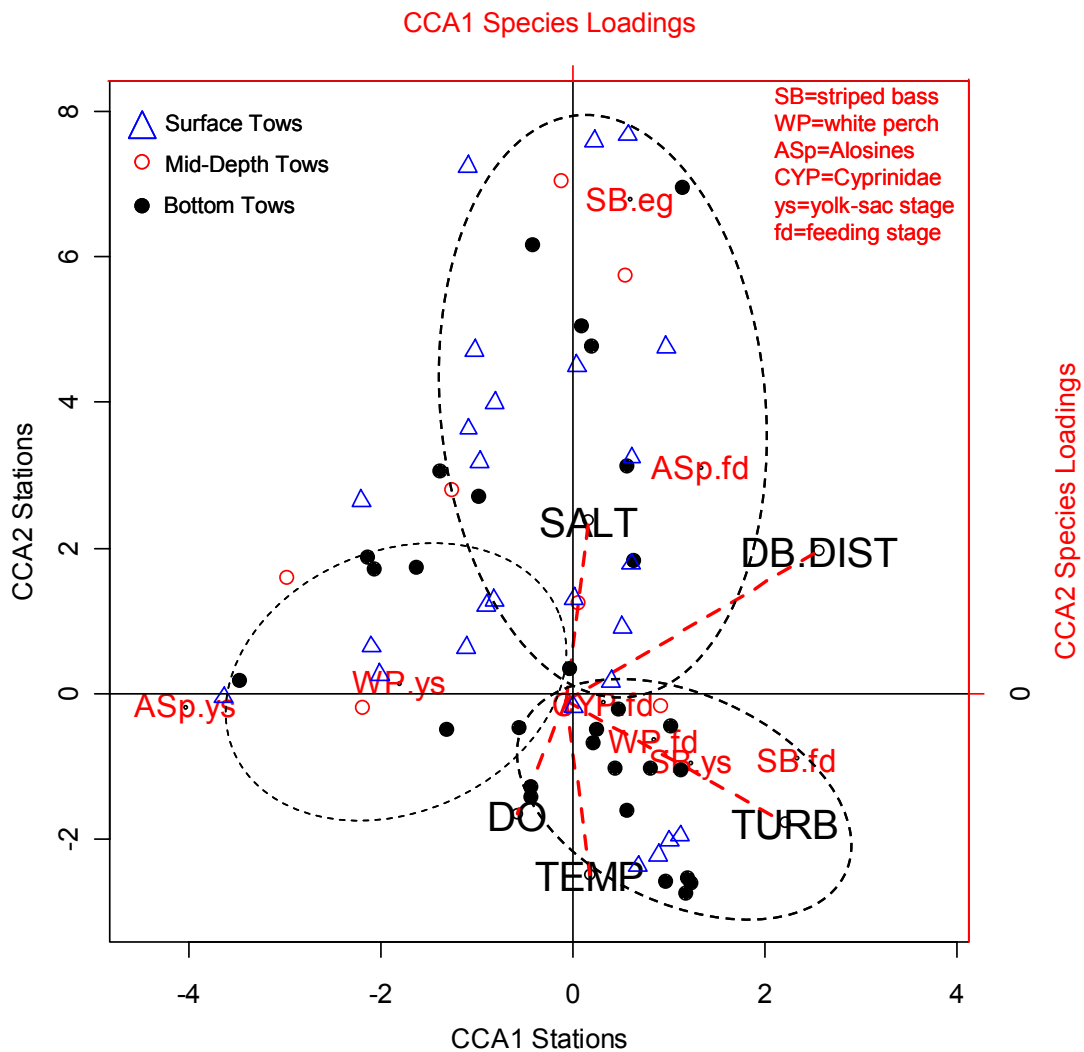


Figure 2-13. Canonical correspondence analysis of BITMAX ichthyoplankton collections and environmental data in May 2003.

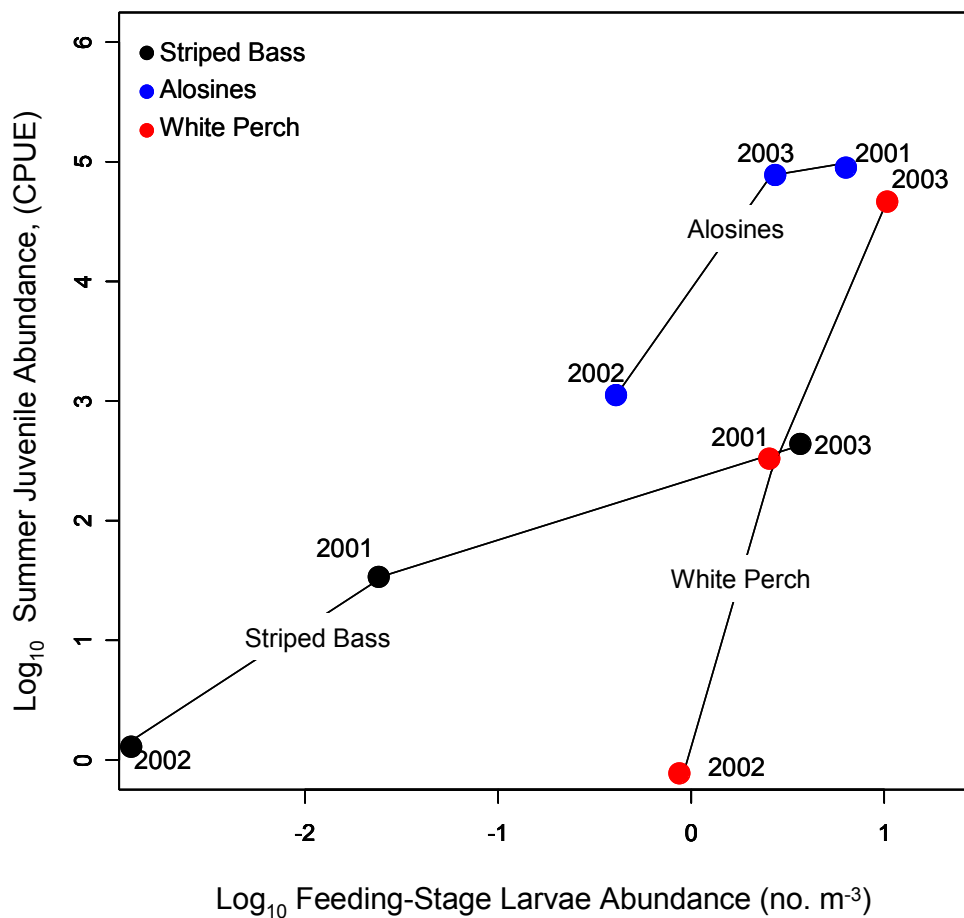


Figure 2-14. Abundances, Upper Chesapeake Bay. Relationship between larval-stage abundance during May and juvenile-stage age-0 abundance during July. BITMAX cruises for ichthyoplankton were conducted in May, and juveniles were sampled in July of each year.

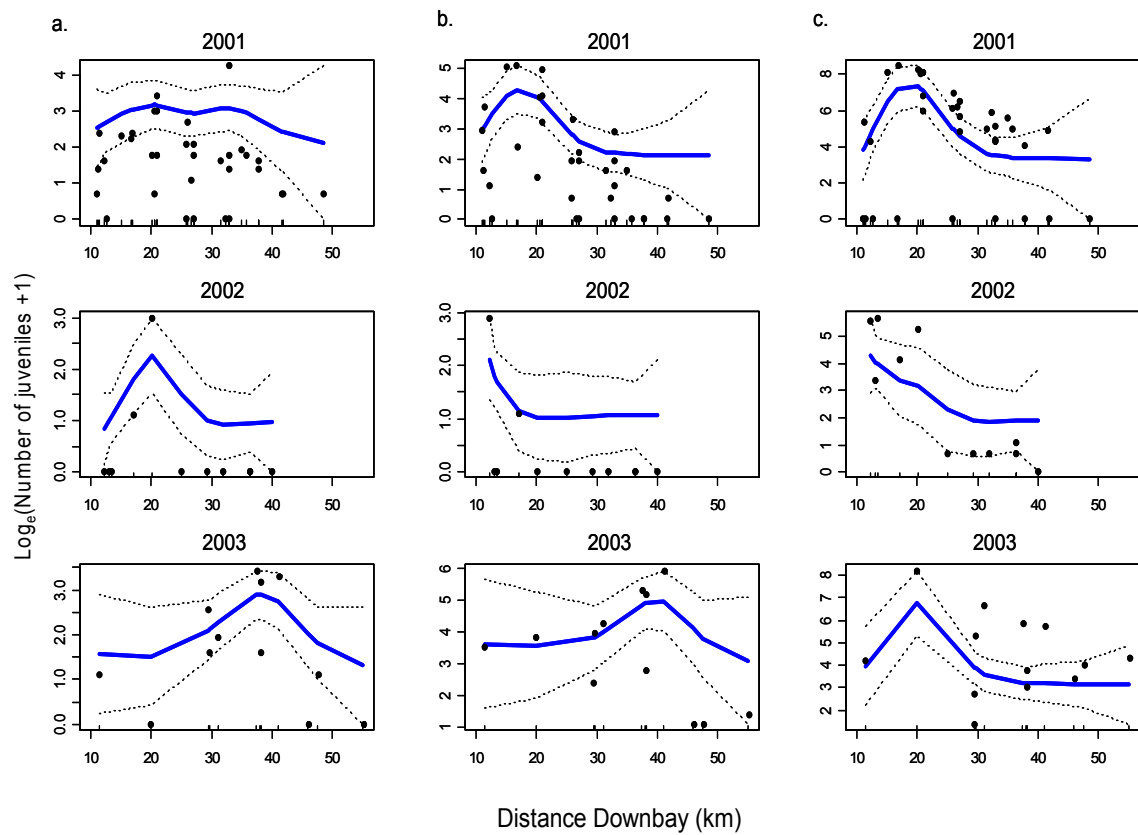


Figure 2-15. Distribution of a) striped bass, b) white perch, and c) alosine, age-0 juveniles in upper Chesapeake Bay during July in the years 2001, 2002, and 2003. Values on y-axis are numbers of juveniles collected in a midwater trawl and curves are based on smooth fits from generalized additive models (GAMS) using downbay distance (km) as a predictor. Note different scales on y-axes.

CHAPTER THREE

Spatial and temporal availability of zooplankton prey coarsely controls striped bass recruitment in upper Chesapeake Bay

INTRODUCTION

Research on recruitment variability has emphasized the connection between larval survival and prey availability since Hjort (1914) proposed a critical life stage and period at the onset of larval feeding that could determine year-class strength. Refinements of the critical-period hypothesis into the match-mismatch hypothesis incorporated the degree of temporal overlap between the spring zooplankton bloom and larvae as a critical determinant of recruitment strength (Cushing, 1990). Together, these hypotheses have motivated research on recruitment variability for decades. Inherent to both hypotheses was the recognition that higher prey concentrations result in enhanced encounter rates between larvae and prey, higher larval growth rates, and increased larval survival. Further extensions of the hypotheses highlighted the importance of growth and stage durations (Houde, 2008) such that larvae encountering sufficient prey would not only have lower probability of starvation but would grow faster, thereby minimizing time in life stages most vulnerable to predation (Houde, 1987; Bailey and Houde, 1989). Measures of larval growth generally are insufficient to explain or predict recruitments but growth and growth-related factors often are correlated with recruitment potential (Houde, 1997).

Spatial variability in prey available to larvae, while not explicitly formalized in recruitment hypotheses, is implicitly important as a determinant of growth and survival. Feeding conditions of larval fish across mesoscale (> 1 km to 100 km) gradients in prey is a consequence of prevailing circulation patterns and frontal features, and interacting spatial dynamics of predator and prey (Munk, 2007). Fish larvae cannot control their distributions over distances exceeding several meters to exploit favorable feeding conditions. For example, striped bass larval swimming speeds approach the upper limit for fish larvae and larvae still only cover distances at a rate of roughly $.03 \text{ m s}^{-1}$ or 3-4 body lengths s^{-1} (Meng, 1993). Thus, a spatial mismatch could occur if peak concentrations of larvae and prey do not co-occur (Chick, 1997). The negative consequences of a spatial mismatch would resemble consequences resulting from a temporal mismatch.

Fronts are features in marine ecosystems that have the potential to aggregate prey and enhance feeding opportunities and growth of fish larvae. For example, both prey availability and larval cod growth were enhanced at a tidal front in the North Sea (Munk, 2007). Similarly, feeding of Japanese sand lance *Ammodytes personatus* on ciliates was enhanced at the convergence of a thermohaline front in the Ise Bay in Japan (Nagano et al., 2001), and condition and growth of larval dab *Limanda limanda* was highest in a tidal-mixing front off the coast of the Isle of Man (Lee et al., 2007). A study focused on larval sprat *Sprattus sprattus* across a tidal front off the west coast of Denmark revealed elevated larval densities at the front, and enhanced larval growth within the mixed area of the front (Munk, 1993). Upwelling and retention areas off the southeast Sicilian coast were associated with high recruitments of Sicilian Channel

anchovy *Engraulis encrasicolus* (Garcia-Lafuente et al., 2002), while mesoscale eddies off the Kuroshio Current enhanced copepod production and were associated with strong recruitments of Japanese anchovy *Engraulis japonicus* (Nakata et al., 2000). Larvae of blue whiting *Micromesistius poutassou* off the west coast of Ireland in a frontal water mass above an offshore bank benefited by utilizing this favorable feeding environment (Hillgruber and Kloppmann, 1999). Survival of yellowfin tuna *Thunnus albacares* larvae in the Mississippi River plume was enhanced in the plume front (Lang et al., 1994).

The structure and dynamics of estuarine fronts and transition zones can affect growth and survival of anadromous fish larvae. In Chesapeake Bay and the St. Lawrence River, there is evidence of a link between survival of anadromous fish larvae, e.g., rainbow smelt *Osmerus mordax* and striped bass *Morone saxatilis*, and dynamics of the estuarine turbidity maximum (ETM) and salt front (Dodson et al., 1989; Sirois and Dodson, 2000a, 2000b; North and Houde, 2001, 2003, 2006). The ETM is a convergence zone located at the head of many coastal plain estuaries (Schubel, 1968). My research was conducted in the estuarine turbidity maximum (ETM) of upper Chesapeake Bay. In Chesapeake Bay, the ETM is a favorable nursery zone for striped bass and white perch larvae (North and Houde, 2001), possibly because elevated concentrations of the copepod *Eurytemora affinis*, a common prey of these larvae, is abundant in and near the ETM (Boynton et al., 1997; North and Houde, 2001; Roman et al., 2001). It is hypothesized that striped bass eggs and larvae are transported to and then retained within the ETM where their survival is enhanced

(North and Houde, 2001, 2003) by high foraging success on *E. affinis* (Roman et al. 2001; North and Houde 2006).

The link between larval striped bass growth and survival and prey availability has been investigated (Ulanowicz and Polgar, 1980; Eldridge et al., 1982; Logan, 1985; Setzler-Hamilton et al., 1987; Tsai, 1991; Cowan et al., 1993; Rutherford and Houde, 1995; North and Houde, 2003). Overall, evidence that prey availability is a major factor shaping year-class success in striped bass is convincing, although most is correlative, with high abundances of prey coinciding with high recruitments. An individual-based model simulating Potomac River striped bass supported the hypothesis that variability in prey availability to larvae could generate 10-fold variability in recruitment (Cowan et al., 1993).

Earlier research on recruitment variability in Chesapeake Bay striped bass evaluated effects of environmental conditions on survival of weekly egg and larvae cohorts (Rutherford and Houde, 1995; Secor and Houde, 1995; McGovern and Olney, 1996). North and Houde (2003, 2006) initiated research to explain spatial variability in egg and larval distributions relative to the salt front and ETM in Chesapeake Bay. I investigated biophysical controls and associated spatial variability in processes controlling prey availability and larval survival among years. Specifically, I analyzed and explained the distribution of striped bass larvae relative to environmental gradients, and spatial and temporal variability in zooplankton concentrations in years of contrasting hydrological conditions in the upper Bay. The analysis included new data for years 2001-2003 and a synthetic, retrospective analysis of data from 1996,

1998 and 1999. The synthesis focused on the role of hydrological variability in the ETM region and its probable effects on recruitment processes in striped bass.

The four objectives of this chapter are to demonstrate how hydrological conditions 1) control distribution of striped bass larvae in the upper Bay, 2) facilitate spatio-temporal overlap with mesozooplankton prey, 3) enhance larval-stage feeding success, and 4) contribute to variability in growth, production, and year-class strength. This research focuses on the broad question, “Does availability of mesozooplankton prey control striped bass recruitment in upper Chesapeake Bay?” The three specific hypotheses are: 1) Feeding success of striped bass larvae is enhanced in wet years, generally characterized by strong recruitments, 2) Larvae and zooplankton prey occur further downbay, are more associated with the ETM and salt front, and exhibit a higher degree of spatial overlap in wet, strong recruitment years, and 3) The seasonal timing in production and availability of zooplankton prey is important for larval survival, and late-spring peaks during May are associated with strong recruitments.

MATERIALS AND METHODS

Research Surveys

Research surveys in the upper Chesapeake Bay were conducted during April and May 1996, 1998-1999, and 2001-2003 (Figure 3-1). The location of the ETM and salt front were determined for each cruise based on a CTD hydrographic survey. Based on the hydrographic surveys, stations were selected to map gradients in

ichthyoplankton abundances throughout the upper Bay and especially above, within, and below the ETM and salt front (Figure 3-1). A CTD cast to profile temperature, salinity and turbidity in the water column preceded ichthyoplankton sampling at each station. The ETM location and its center were defined as the geographic range (typically 5-10 km) and mid point of that range, respectively, where maximum turbidity levels occurred.

Ichthyoplankton was sampled with an opening-closing, 1-m² Tucker trawl with 280-um meshes fished in three discrete depths. The amount of water filtered by a 2-min tow in each depth stratum was, on average, 126 m³. All striped bass eggs and larvae were identified and enumerated from samples and expressed as number of eggs or larvae per cubic meter.

The distributions of striped bass eggs and larvae were analyzed using two approaches. First, egg and larvae data were pooled from all surveys to evaluate average annual, stage-specific distribution patterns. This initial analysis was motivated by earlier observations (Chapter 2) of the strong positive relationship between mean spring freshwater discharge and year-class strength (North and Houde, 2001), suggesting that effects attributable to inter-annual variability in flow surpassed effects attributable to flow variability at shorter time scales. Egg and larvae concentrations were averaged in 5-km bins and standardized as z-scores (residual divided by standard deviation) to emphasize centers of abundance for particular stages. This analysis did not include data from 1996 because eggs and yolk-sac larvae of striped bass were not sampled sufficiently in this year. The second approach emphasized analysis of individual survey data from the three most recent years (2001-

2003) to rigorously evaluate distribution patterns relative to upper Bay hydrographic structure.

Zooplankton Abundance and Distribution

Inter-annual and spatial variability in occurrences of zooplankton that serve as prey for striped bass larvae was analyzed in the upper Bay. Most analyses on mesozooplankton focused on the two dominant prey of striped bass larvae, the calanoid copepod *Eurytemora affinis* and the cladoceran *Bosmina longirostris*. Common prey of striped bass larvae and congener white perch larvae in the upper Bay (Shoji et al., 2005) include the copepodite and adult-stages of calanoid copepods *Eurytemora affinis* and *Acartia tonsa* and juvenile and adult stages of the cladoceran *Bosmina longirostris*. *Eurytemora affinis* and *B. longirostris* had been reported previously as dominant prey of striped bass larvae (Beaven and Mihursky, 1980; Campfield, 2005). These two prey organisms are proposed to be most important for larval survival and recruitment success of striped bass (Limburg et al., 1999; Wood, 2000). Inter-annual differences in the distributions *E. affinis* and *B. longirostris* were evaluated. Additionally, spatial (1996, 1998, 1999, 2001-2003) and temporal (1993-2002) patterns in the combined concentrations of these taxa were evaluated and compared to minimum prey thresholds. I compared the combined concentration of prey (*E. affinis* and *B. longirostris*) to minimum prey thresholds based on three laboratory studies, including one that tested *Artemia* nauplii as prey (Eldridge et al., 1981), one that tested *Eurytemora* nauplii and other life stages (Tsai, 1991), and one

using a natural assemblage of zooplankton from Lake Marion, South Carolina (Chick and Van Den Avyle, 1999).

Broad inter-annual trends in spring zooplankton abundance and distribution were evaluated by analyzing April and May samples collected by the Chesapeake Bay Program (Table 3-2). Data from four CBP monitoring stations in the upper 75km of the Bay were analyzed (Figure 3-2). These stations were sampled once in April and twice in May during all years. Because the CBP zooplankton monitoring program was terminated in 2002, zooplankton analysis in 2003 was based on estimated abundances obtained from high-frequency acoustics (see below). Three of the four CBP stations were located within the primary striped bass nursery and one station (CB4.3c) was located 10-15 km downbay. Zooplankton was sampled in duplicate stepped-oblique tows with paired (202 μ m mesh). For analysis, the number of *Eurytemora* copepodites and adults, number of *Bosmina* juveniles and adults, and the sum of these prey types were standardized as number of individuals per cubic meter of water sampled.

In 2003, the Tracor Acoustic Profiling System (TAPS) was used to provide estimates of zooplankton abundance and distribution. The TAPS instrument was mounted on the CTD. The TAPS records depth and acoustical volume back-scattering strength (Sv) at 6 transducer frequencies (265, 420, 700, 1100, 1850 and 3000 kHz)(Holliday and Pieper, 1995). I analyzed TAPS zooplankton lengths between 0.5 and 1.4 mm, or equivalent spherical radii (ESR) between 0.06 to 0.25 mm to represent the size range of zooplankton prey typically consumed by striped bass larvae. I averaged the TAPS estimates of particles for the entire water column to provide an estimate of total prey concentration. In the designated size range and at locations

where TAPS was deployed, the estimate of total prey would mostly consist of *E. affinis* and *B. longirostris*, based on numerical dominance of these taxa in plankton tows from other year. In 1996 and 2003, the two wettest years during this research, estimates of zooplankton abundances were derived from a comparison of net catches and acoustics, respectively. The consistency of the comparisons in 1996 (Roman, 2001) and rather similar TAPS estimates in 2003 indicate that the acoustics estimates are acceptable.

To examine inter-annual and spatial differences in trends and patterns of total zooplankton along the channel axis of the upper Bay, concentration data were fit with a loess smoothing function (span = 0.7, degree = 1). The loess fits helped to define trends, which usually were not linear or monotonic and had conspicuous peaks in most years. Observed zooplankton concentrations, mean values based on loess fits, and standard errors of these fits are reported.

Loess fits (span = 0.7, degree = 1) of larval striped bass concentrations also were developed to compare overlap with the zooplankton fits (i.e., to delineate probable predator-prey relationships). The degree of spatial overlap between zooplankton and larvae was evaluated each year. In addition, mean annual concentrations of zooplankton were calculated for 1) the entire upper Bay, 2) for the area exclusively where larvae occurred, and 3) for the area where maximum larval concentrations occurred. Correlation statistics between mean zooplankton concentrations during the period of peak larval-stage striped bass production (April-May), and at locations where most striped bass larvae occurred, and age-0 juvenile recruitment indices (mean

abundance July through September) were used to evaluate the relationship between zooplankton prey availability and recruitment success.

The timing of the spring zooplankton peak, based on the zooplankton monitoring by the Chesapeake Bay Program, and possible effects on striped bass recruitment also were evaluated. Zooplankton sampled in the striped bass nursery area during the March to June period were included in the analysis (Table 3-2). For this analysis, concentrations of *E. affinis* and *B. longirostris* were expressed as means by ordinal day to evaluate inter-annual differences in seasonality. In addition, the concentrations of *E. affinis* and *B. longirostris* were pooled to evaluate inter-annual variability in seasonal timing of total prey available.

Diet Analyses

Diet analysis was conducted on striped bass larvae collected from 2001-2003. Standard length (SL) of larvae was measured to the nearest 0.1 mm. Gut contents (n=185) were removed under a dissecting microscope and identified. In samples with 5 or fewer larvae, gut contents of all larvae were analyzed. In samples with 5 to 25 larvae, between 5 and 10 individuals were randomly selected for stomach analysis. Each prey item was identified and measured (length) using an ocular micrometer.

The effect of larva size on feeding success (mean number of prey items per gut) was determined in a general linear model (GLM) analysis. ANCOVA was applied to compare feeding success between years using larval standard length as a covariate. Larvae were separated into two size classes, < 7.5 mm and ≥ 7.5 mm. At

7.5 mm, the yolk sac is fully absorbed and teeth are easily visible, indicating obligate external feeding by this size and stage of development (Mansueti, 1958); there was a conspicuous increase in the mean number of prey per gut in larvae > 7.5mm. Analyses evaluating abiotic effects and spatial differences in feeding success were conducted on each larval size class. The level of significance and parameter estimates were reported based on the GLM analysis.

RESULTS

Recruitment Variability and Freshwater Flow

Freshwater discharge into the upper Bay during spring months (March and April) varied >2-fold among the six years of this research (Figure 3-3), with highest averaged flows in 1998, 2003, and 1996, lowest flows in 1999 and 2002, and moderate flows in 2001. Abundances of feeding-stage, striped bass larvae were significantly higher (Kruskal-Wallis test, $p < 0.05$) in 2003 (mean = 3.7 m^{-3}), 1996 (mean = 2.5 m^{-3}), and 1998 (mean = 0.1 m^{-3}) when freshwater flows were highest. Feeding-stage larval abundances were significantly lower in 1999 (mean = 0 m^{-3}) and 2002 (mean = 0.0015 m^{-3}) when freshwater flow was much reduced.

A multiple regression model successfully described recruitment levels of YOY striped bass at four months of age from 1985 to 2003 and forecasted recruitment levels for years 2004-2007 (Figure 3-4). A suite of abiotic and biotic variables were considered for inclusion as independent variables in the initial model, but only spring freshwater flow and spring temperature were significant ($p < 0.05$) and retained in the

final model. The model described recruitment reasonably well ($R^2 = 0.72$), and was used with good success to forecast recruitment for the most recent four years.

Egg and Larval Distribution and Response to Hydrological Variability

On average, egg distributions were similar in the five years examined (1998, 1999, 2001-2003). Egg occurrences were not associated with the ETM or salt front in any year (Figure 3-5), although, inter-annual differences in hydrological conditions affected their distribution. Eggs were patchily distributed and occurred over a relatively broad geographic range ($>25\text{km}$) that extended downbay into the ETM and salt front in 1999 and 2002 when hydrological conditions were dry (Figure 3-5). In contrast, the distribution of eggs in 2003, the wettest year, was clearly upbay (15-20km) and better defined (Figure 3-5) compared to other years .

The distribution of yolk-sac and feeding-stage larvae of striped bass varied considerably between years, a reflection of inter-annual differences in hydrological conditions (Figure 3-5). In years of high freshwater discharge during March and April, the annually-averaged center of larval abundance was further down-estuary and more associated with the ETM (1998 and 2003) (Figure 3-5). In contrast, when freshwater discharge was below average (2002), yolk-sac and feeding-stage larvae were most abundant up-estuary and were less associated with the ETM (Figure 3-5). However, some yolk-sac larvae were collected within the ETM and at moderately high salinities (3-5) in this dry year (2002) (Figure 3-6). No feeding-stage larvae were collected in 1999, but yolk-sac larvae were collected far upbay in this dry year.

Larval distributions in the three most recent years (2001-2003) differed conspicuously inter-annually. In 2001, there were distinct centers of feeding-stage and yolk-sac larvae abundances located upbay of, but extending down-estuary to, the salt front and near the ETM (Figure 3-6). In the dry year 2002 (Figure 3-6), feeding-stage larvae were again most abundant well upbay of the front. However, in contrast to their distribution in 2001 they did not extend downbay into the salt front and ETM. There were patches of yolk-sac larvae in 2002 throughout the study location and extending downbay to the ETM and below the salt front. In 2003, a very wet year, there was a center of yolk-sac and feeding-stage larvae abundance nearly 15 km further downbay compared to 2001 and 2002 (Figure 3-6). Moreover, both yolk-sac and feeding-stage larvae were strongly associated with the salt front and ETM in 2003 (Figure 3-6). Larval distributions also varied between surveys conducted within years, although inter-annual differences were more pronounced.

As a generalization, larvae were located further downbay in moderate to high freshwater discharge years ($r^2=0.37$, n.s.) (Figure 3-7a). In high-flow years, larvae also appeared to be more associated with the salt front and ETM ($r^2=0.39$, n.s.) (Figure 3-7b). In contrast, larvae generally occurred further upbay and were less associated with the ETM in years when freshwater flows were lower (Figure 3-7a,b). These relationships were not significant at the $p=0.05$ level, probably because of the limited number of years ($n=6$) available for this analysis.

Intra-annual variability in hydrology acts to control transport and retention of striped bass eggs and yolk-sac larvae. Outcomes can be variable and complex. For example, during the dry year 2002, freshwater discharge was far below average during

March and April (Figure 3-8a,b). However, in May 2002, the month of my survey, discharge levels were the highest observed in these years (Figure 3-8c). Low flows during March-April 2002 set up conditions typical for low discharge years, with centers of feeding-stage larvae occurring further up-estuary and few feeding-stage larvae associated with the ETM (Figure 3-8d,e). The elevated discharge during May 2002 apparently disrupted the hydrographic structure and larval distributions. In May 2002, it is probable that a down-estuary shift in egg and yolk-sac larvae distribution occurred just prior to the research cruise owing to enhanced down-estuary transport of eggs and yolk-sac larvae or a change in preferred spawning location by adult striped bass. In May 2002, the distribution of feeding-stage larvae that had been hatched many days earlier, under low-flow conditions, remained up-estuary far from the ETM (Figure 3-8d,e), while large numbers of younger yolk-sac larvae were down-estuary near the ETM (Figure 3-8c).

Diet and feeding success

Larval striped bass in upper Chesapeake Bay fed almost exclusively on two prey species, the cladoceran *Bosmina longirostris* and the calanoid copepod *Eurytemora affinis*. All other prey taxa, including the cladoceran *Daphnia* spp., the calanoid copepod *Acartia tonsa*, and cyclopoid copepods in the genus *Oithona* were rare and occurred in less than 5% of larval guts. Feeding success was higher in 2003 than in 2001, based on both number of prey per larval gut ($p < 0.01$) and prey incidence

in guts ($p < 0.001$) (Figure 3-9). Too few feeding-stage larvae were available for analysis in 2002.

The most notable difference in diet between years was the increased importance of the cladoceran *B. longirostris* in 2003, the year when average freshwater discharge was highest. The percentage of larvae that consumed *Bosmina* increased from $<22\%$ in 2001 to 50% in 2003. The number of *Bosmina* consumed per larva in 2003 was also significantly higher than in 2001 ($p < 0.001$) (Table 3-3). Feeding on both *Bosmina* and the copepod *Eurytemora* was significantly higher in 2003, although inter-annual differences in consumption of *Bosmina* were more pronounced than inter-annual differences in consumption of copepods (Table 3-3).

Overall, number of prey in guts of larval striped bass was directly related to larval size ($p < 0.0001$) (Table 3-3). Evaluation of feeding success with respect to larval size within years indicated that feeding was positively related to larval length in 2001 ($p < 0.001$), but not in 2003 when numbers of prey per gut were relatively high for larvae of all lengths (Figure 3-10). The results indicate that small, first-feeding larvae fed less successfully than larger, older larvae in 2001 and, importantly, small (< 7.5 mm) larvae in 2001 fed less successfully than small larvae in 2003.

Environmental factors affected feeding success of small (< 7.5 mm) and large (≥ 7.5 mm) larvae. During 2001, when most larvae occurred above the ETM, only the location variable, i.e., distance downbay, affected feeding success (Table 3-3). Feeding success of ≥ 7.5 mm larvae on copepods increased ($p < 0.05$) downbay in 2001, probably because of the relatively high *Eurytemora* concentrations near the salt front and ETM (Figure 3-12). Larvae having highest feeding success in 2001 were located

downbay from the location of maximum larval abundance. Feeding by <7.5mm larvae in 2001 was not affected by any measured environmental factor, a result apparently attributable to the generally poor feeding success of small larvae in 2001.

In 2003, there were location- and size-specific differences in the amount and types of prey consumed by striped bass larvae. Most larvae occurred downbay, and were associated with the ETM in 2003. Mean number of prey per small (i.e. < 7.5 mm) larva declined with respect to distance downbay, salinity, and turbidity for small larvae (Table 3-3). The negative relationships between feeding success of small larvae and environmental factors in 2003 were apparent for total prey and for *Bosmina*, but not for *Eurytemora*. Spatial trend in the mean number of *Eurytemora* per gut in large larvae in 2003 was similar to 2001. Feeding on *Eurytemora* increased downbay ($p<0.05$) and at higher salinities ($p<0.05$) (Table 3-3). As a consequence, larger larvae in 2003 fed more successfully on *Eurytemora* at downbay locations where most larvae occurred. In contrast, feeding on *Bosmina* by large and small striped bass larvae was more successful further upbay ($p<0.0001$), at lower salinities ($p<0.0001$), and lower turbidities ($p<0.05$).

Spatio-temporal overlap in striped bass larvae and zooplankton prey

The distribution of zooplankton serving as prey for larval striped bass in upper Chesapeake Bay is strongly controlled by hydrological conditions. Maximum aggregate concentrations of the dominant upper Bay mesozooplankters, *Eurytemora affinis*, *Bosmina longirostris*, and *Acartia tonsa*, were located further downbay

($p < 0.01$, $r^2 = 0.59$) during years of high freshwater discharge (Figure 3-11).

Concentrations of *E. affinis* were higher at upbay locations in dry years (e.g., 1999 and 2002) but were higher at downbay locations, peaking at or below the salt front and ETM, in years of moderate to high freshwater discharge (Figures 3-11 and 3-12). Maximum *B. longirostris* concentrations occurred up-estuary of the salt front and ETM in all years. However, in years of moderate and high freshwater discharge *B. longirostris* tended to occur further downbay and the degree of overlap with the ETM increased (Figure 3-12).

Hydrological variability affected larval striped bass and zooplankton distributions. During two dry years, 1999 and 2002, the combined concentrations of *Eurytemora* and *Bosmina* almost always were below minimum levels of prey believed to be necessary for production of striped bass larvae (approximately 50,000 individuals m^{-3}) at all locations in the upper Bay (Figure 3-13). Recruitments of YOY striped bass were well below average (1.9 and 1.4 per seine haul, respectively) during these two dry years (see Ch 5).

In 1998 and 2001, zooplankton concentrations were higher. Mean freshwater discharges during March and April were high and near average in 1998 and 2001, respectively (Figure 3-3), when YOY recruitments of striped bass were moderate (4.3 and 7.2 per seine haul, respectively, see Ch 5). Zooplankton concentrations exceeded the minimal prey thresholds and reached 50,000 individuals m^{-3} at some locations in the upper Bay during 1998 and 2001, but most striped bass larvae occurred upbay of the peak prey concentrations and, as a result, did not experience favorable feeding conditions (Figure 3-13).

In 1996 and 2003, two wet, high-discharge years, zooplankton concentrations were considerably higher throughout the upper Bay (Figure 3-3). Prey concentrations exceeded 100,000 individuals m^{-3} near the ETM. Freshwater discharge levels and YOY striped bass recruitments were also high in 1996 and 2003 (15.0 and 11.9 per seine haul, respectively, see Ch 5). Most importantly, there was a high degree of spatial overlap between zooplankton and striped bass larvae during these two years (Figure 3-13). Zooplankton concentrations were above the minimum threshold level of 50,000 m^{-3} at all locations where larvae occurred, and were at least twice as high as the most rigorous minimum prey level of 100,000 m^{-3} at locations where most striped bass larvae occurred (Figure 3-13). Correlations between YOY striped bass recruitments in July through September and overall spring zooplankton concentrations in the upper Bay were positive, but non-significant and weak (Table 3-5). However, correlations between YOY recruitment levels and concentrations of zooplankton at the specific locations coincident with larval striped bass occurrences were very strong and significant ($p < 0.05$, $r^2 > 0.74$).

There was substantial temporal variability in occurrences of dominant zooplankton prey, with probable consequences to feeding success and survival of striped bass larvae. The seasonality of the cladoceran *Bosmina* varied little among years (Figure 3-14). The development of a *Bosmina* bloom commenced between late April and early May when concentrations increased markedly. Peak concentration of *Bosmina* usually occurred during early June, or at dates later than examined in my research. The seasonality of the copepod *Eurytemora* varied considerably among

years. Its concentrations usually peaked before May (ordinal day = 120) and declined thereafter (Figure 3-14).

The degree of temporal overlap between the two zooplankters and the period when most striped bass larvae occur was largely driven by variability in seasonality of *Eurytemora*. Overlap with striped bass larvae was enhanced when *Eurytemora* peaked during May rather than earlier in March or April, or when concentrations of *Eurytemora* remained high in May despite peaking at an earlier date.

Feeding conditions for striped bass larvae as judged by temporal overlap with zooplankton show considerable variability (Figure 3-14). Peak concentrations of striped bass larvae occur during late April through mid-late May (ordinal days 110-140) in upper Chesapeake Bay. Spring zooplankton concentrations peaked within this 30-day interval in only two years (1996 and 2003) during the period 1993-2002 (Figure 3-14). The late-season peaks in spring zooplankton concentrations in 1993 and 1996 were strongly associated ($r^2=0.72$, $p<0.0001$) with very high recruitment levels (Figure 3-15). In contrast, zooplankton concentrations peaked four weeks earlier (before April 1) in most years and then quickly declined. In those years, age-0 recruitments of striped bass were generally low.

Prey availability is a major determinant of striped bass larval survival and recruitment in upper Chesapeake Bay. There are strong relationships between age-0 juvenile abundance and both the spatial (Table 3-5; Figure 3-13) and temporal availability of prey (Figures 3-14 and 3-15). However, neither spatial nor temporal coincidence with prey alone is sufficient to support strong recruitments. High temporal overlap of striped bass larvae with prey during a year with low or moderate

freshwater flow results in suitable prey at some locations in the upper Bay but not necessarily where most larvae occur. For example, in 2002 the timing of peak prey was sufficient to support larval feeding, but prey concentrations were low throughout the upper Bay, presumably due to low freshwater flows during early spring (Figures 3-13, 3-14). Similarly, in 2001 peak zooplankton concentrations overlapped and matched the period of striped bass larval occurrence (Figure 3-14). But, freshwater flows during the months January through May were below average and larval striped bass primarily occurred upbay of the ETM and salt front (Figure 3-13) in water with low zooplankton concentrations. In 1998, freshwater flows were very high and larvae were located (Figure 3-13) near the ETM, but *E. affinis* concentrations in the larval nursery area had peaked earlier, during late March, and temporal overlap with striped bass larvae was minimal (Figure 3-14).

DISCUSSION

Environmental Conditions, Prey Availability, and Recruitment

Striped bass recruitment success in upper Chesapeake Bay is largely determined by annual differences in hydrological conditions. Biophysical controls of recruitment include both direct and indirect effects of hydrological variability on egg and larval survival. The outcome of direct effects (e.g. reduced retention of larvae, osmotic stress) are most conspicuous during dry years (e.g. 1999 and 2002) when recruitments of striped bass are very poor, whereas indirect effects (attributable to

trophodynamics) distinguish years when recruitments are moderate (e.g., 1998 and 2001) and strong (e.g., 1996 and 2003). In the two dry years (1999 and 2002), there were very low abundances of feeding-stage larvae, and most were collected >15 km above the salt front and ETM. The low numbers of feeding-stage larvae at the salt front and ETM in 1999 and 2002 could reflect an upbay shift in the location of adult spawning. For example, the position of the salt wedge in the Savannah River in 1986 to 1989 affected spawning site selection by adult striped bass (Van Den Avyle and Maynard, 1994). Alternatively, reduced retention and higher salinities near the ETM and salt front may result in poor survival and down-estuary loss of eggs and larvae in dry years. This mechanism was proposed previously to explain the lack of feeding-stage larvae in 1999 (North and Houde, 2001, North, 2003 #7149).

My analysis and results emphasize the indirect role of trophodynamic effects of hydrological variability, including spatial and temporal matches and mismatches between occurrences of striped bass larvae and zooplankton prey, and consequences for larval feeding success, growth, and survival. Prey availability is a major determinant of larval striped bass survival and recruitment in upper Chesapeake Bay. My results support the three hypotheses: 1) feeding success of striped bass larvae is enhanced in wet, strong recruitment years, 2) larvae and zooplankton prey occur further downbay, are more associated with the ETM and salt front, and exhibit a higher degree of spatial overlap in high freshwater-discharge years, and 3) the seasonal timing of peak zooplankton prey is important for larval survival. In general, enhanced spatio-temporal availability of zooplankton prey promotes higher larval

feeding success and growth rates (Chapter 4), increased cumulative larval-stage survival, and strong recruitments of striped bass in the upper Chesapeake Bay.

Prey availability alone may have accounted for the observed variability in YOY striped bass recruitment during this study. In the years of this research, prey concentrations coincident with locations of larvae occurrence varied >26-fold, and prey concentrations located near the center of larvae abundance varied >1000-fold (Table 3-4). Larvae were strongly associated with the ETM in 1996 and 2003, the two strongest recruitment years (Figure 3-13) when prey concentrations in the ETM and at the center of larval abundance exceeded 250,000 individuals m^{-3} . Those levels surpassed all reported estimates of threshold prey requirements ranging from 50,000 – 100,000 individuals m^{-3} (Eldridge et al., 1981; Chesney, 1989; Tsai, 1991). In contrast, in poor recruitment years, prey concentrations were lower (average < 2000 m^{-3}) throughout the upper Bay and were usually well below minimum levels required by larvae. Rutherford et al. (1997) proposed that relatively high coincidence of striped bass larvae and zooplankton explained a strong recruitment year in 1989 in the upper Chesapeake Bay. Recruitments of YOY striped bass differed 3-fold between 1988 and 1989. Mean concentrations of zooplankton were twice as high in 1989, the stronger recruitment year.

Temporal and spatial matches in prey availability are necessary to produce the strongest recruitments. A spatial mismatch between striped bass larvae and prey in 2001 (Figure 3-13) may have explained the unexpectedly low recruitment in this year despite a strong temporal match (Figure 3-14 and 3-15). In 1998, freshwater flow was very high and larvae occurred in the ETM, but there was weak temporal coincidence

between peak zooplankton concentrations and larvae compared to 1996 and 2003, the other wet years in this research. In 1998, the spring zooplankton peak apparently occurred nearly 30 days too early to have effectively supported high consumption by striped bass larvae. In contrast, prey availability in 1996 was characterized by a spatial and temporal match with striped bass larvae that was associated with the highest YOY recruitment in the past 22 years. In 2003, there also was strong recruitment of striped bass when high concentration ($> 200,000$ individuals m^{-3}) and distribution of zooplankton in May 2003 were temporally and spatially coincident with feeding-stage larvae..

Spring freshwater flow and temperature are important determinants of striped bass larval survival and age-0 recruitment strength, in part, because of their influence on the feeding conditions for striped bass larvae. The important role of freshwater flow in potentially controlling larval survival of striped bass has been recognized in earlier research in Chesapeake Bay (Kellogg et al., 1996; McGovern and Olney, 1996; North and Houde, 2001; Wood, 2000) and elsewhere (Turner and Chadwick, 1972; Kimmerer et al., 2001). My results confirmed this relationship but, additionally, analyzed its effect on distributions of larvae and zooplankton, and used it to develop predictive relationships. Temperature potentially can control both timing of striped bass spawning and larval emergence (Secor and Houde, 1995), as well as peak production of *Eurytemora* (Wood, 2000). Level of freshwater flow controls abundance and distribution of *Eurytemora* in upper Chesapeake Bay (Kimmel and Roman, 2004; Lloyd, 2006).

Adding prey concentration as a variable to my regression model that describes and forecasts YOY recruitments of striped bass probably would improve its forecasting capability. Unfortunately, this possibility was eliminated when the Chesapeake Bay Program terminated its zooplankton monitoring in 2002 (CB-Program, 2002). The variables in my model to forecast recruitments include spring freshwater flow and spring temperature; both are important indirect determinants of prey availability and provide reasonably good predictive capability for YOY striped bass recruitments. Water temperatures (CB-Program, 2006) and spring flow data are readily available (USGS, 2008) for forecasting future recruitments of striped bass. A prey index that incorporated spatial and temporal availability of zooplankton prey would enhance recruitment forecasting capabilities.

Seasonal Timing of Zooplankton and Recruitment Strength

A temporal match between production of fish larvae and prey appears to be an important prerequisite for strong recruitments in fishes, i.e., the match-mismatch hypothesis (Cushing, 1975). Striped bass is no exception to this rule. Most striped bass larvae hatch during late April and early May in upper Chesapeake Bay (Rutherford and Houde, 1995) in response to temperatures rising above 12 °C (Secor and Houde, 1995). The best temporal match would occur when zooplankton peaks in early May. In upper Chesapeake Bay, peak zooplankton concentrations occur most often in March and April, a mismatch between prey availability and larval striped bass production. The strongly positive relationship ($r^2=0.88$, $p<0.01$) between day of peak

zooplankton concentration and YOY recruitment strength (Figure 3-15) indicates that matches occur in years of late (May) peaking zooplankton production as observed in 1993 and 1996.

There is an apparent climate link between zooplankton production and larval striped bass survival. It was postulated in the 1970s that there is a positive association between cold-wet spring conditions and recruitment of anadromous fish in Chesapeake Bay (Mihursky et al., 1981). Subsequently, it was demonstrated that frequencies of favorable or unfavorable climate patterns control spring temperatures, freshwater flows, and prey available to anadromous fish larvae and juveniles in Chesapeake Bay, including striped bass (Wood, 2000). A climate pattern, the “Ohio Valley High,” during late winter is associated with increased freshwater flows and increased abundances of *Eurytemora affinis* in spring (Wood, 2000; Kimmel and Roman, 2004). *Eurytemora* abundance in Chesapeake Bay usually peaks in March or April (Kimmel and Roman, 2004). In years when the winter-dominant “Ohio Valley High” climate pattern persists through March, the spring zooplankton bloom extends to May, which promotes a match with striped bass larvae (Wood, 2000). In contrast, dominance of another late-winter climate pattern that is associated with warm-dry conditions, the “Azores-Bermuda High,” results in a rapid transition from winter to spring, earlier seasonal peaks in zooplankton, and a mismatch with striped bass larvae.

My results on the temporal variability of striped bass prey in the upper Bay generally agree with interpretations based on climatology. However, there are species-specific differences in the timing of the upper Bay’s spring zooplankton bloom that may have consequences for larval survival. I observed strong recruitments and

enhanced apparent larval survival when the most abundant prey *E. affinis* peaked in late spring (Figure 3-14 and Figure 3-15). In wet years, *Eurytemora* concentrations were considerably lower earlier in the spring (March/April). In contrast, concentrations of the cladoceran *B. longirostris* were always low during early spring but increased during late spring, usually in early May. The predictability in the timing of the *Bosmina* bloom has been reported for the Hudson River where its concentrations invariably surge from 100 to 100,000 individuals m⁻³ from late May through mid-June (Limburg et al., 1997). The strongest temporal overlap between larval striped bass and its two dominant prey, *Eurytemora* and *Bosmina*., in upper Chesapeake Bay occurs when *Eurytemora* peaks during early May. For example, prey levels during May 1996 were among the highest recorded for the 1993-2002 period, although levels during March/April 1996 were >25-fold lower and probably below levels required by striped bass larvae. Recruitment level of striped bass in 1996 was one of the highest recorded over the past three decades, presumably a response to temporal (Figure 3-14) and spatial (Figure 3-13) matches between larval striped bass and zooplankton prey.

Critical period

Although temperature can have a strong effect on growth of larval striped bass (Rutherford and Houde, 1995; Secor and Houde, 1995) and on fish larvae in general (Houde, 2008), it is probable that feeding success and annual growth differences observed in my research result from inter-annual variability in prey availability.

Temperatures experienced by 2003 larvae were cooler (range = 15-16 °C) compared to the warmer (range=16-19 °C) temperatures experienced by larvae in 2001. There is a strong, although variable, relationship between larval striped bass growth and temperature(Rutherford and Houde, 1995) and expected growth of larval striped bass would be higher in 2001 than in 2003 based only on annual differences in temperature. But, growth rates of small larvae were similar in the two years and growth of older larvae (>12 dph) was higher in 2003 (Chapter 4), suggesting that enhanced prey availability and feeding success were responsible. Observed feeding success of striped bass larvae (Figure 3-9) was higher in 2003, when most larvae were located close to the ETM, than in 2001.

Recruitment in Chesapeake Bay striped bass is coarsely controlled by survival during the larval stage. Uphoff (1989) and Rutherford and Houde (1997) correlated striped bass YOY recruitment levels and larval abundances, and reported that recruitment is fixed during the early postlarval stage (8-10 mm). Inter-annual differences in ratios of G/Z (weight-specific growth rate to instantaneous mortality rate) at 8-mm length were positively correlated with larval survival (Secor and Houde, 1995; Houde, 1996; Rutherford et al. 1997) and with YOY juvenile recruitment indices (Rutherford et al., 1997). In synthesis research evaluating $M (=Z)$ and G in five cohorts of striped bass larvae, the sizes of striped bass larvae at which cohorts began to gain biomass ($M/G \geq 1.0$) was variable and sensitive to environmental conditions (Houde, 1997). Cohorts attaining $M/G < 1.0$ at the smallest size (≤ 7.7 mm) potentially contribute higher numbers and biomass (i.e. stronger year classes) to recruited striped bass populations. Thus, environmental factors that control prey

availability and larval-stage G, especially for small, feeding-stage larvae (< 7.7 mm), may play a major role in determining year-class strength of striped bass.

In my research, the combined results of prey availability, feeding success (Figure 3-9 and Figure 3-10) and growth-rate variability (Chapter 4) lend further support to evidence that the early-feeding stage (< 7.5 mm) represents a critical stage in determining year-class strength of striped bass. Moreover, my findings identify a mechanism related to freshwater flow, temperature, and spatio-temporal variability in prey that explains the observations.

The ETM and Recruitment Success

Striped bass larvae were more likely to be found in the ETM during strong recruitment years, suggesting a connection between the ETM, freshwater flow, and striped bass recruitment. Earlier research on larval retention and survival in the upper Bay's ETM region led to the hypothesis that freshwater flow controls recruitment by affecting overlap of temperature/salinity zones preferred by later-stage larvae with elevated productivity in the ETM (North and Houde, 2001, 2006). My results are generally consistent with this hypothesis, although larval striped bass are not closely associated with the ETM in all years. Freshwater discharge exerts strong control over the location of yolk-sac and feeding-stage striped bass larvae. Both yolk-sac and feeding-stage larvae occurred more than 20km further down-estuary in 2003, a year of higher freshwater discharge, than in 2002 when freshwater flows were lower.. The downbay displacement of striped bass larvae in wet years enhanced the degree of

overlap between larvae and the ETM. Recruitment strength was nearly 9-fold higher in 2003 when most larvae occurred in the ETM, compared to the strength of recruitment in 2002. Enhanced larval survival in years of high freshwater flow appears to result from higher proportions of larvae occurring within the favorable conditions of the ETM (North and Houde, 2003; Martino and Houde, 2004; North and Houde, 2006).

Physical forces associated with high freshwater flows aggregate larval striped bass and zooplankton prey at the salt front and ETM where larvae benefit from higher feeding success and survival. High freshwater flows are associated with enhanced estuarine gravitational circulation and retention at the salt front and ETM (Hetland and Geyer, 2004). During wet years when gravitational circulation is enhanced, concentrations of *Eurytemora* increase, and its center of its abundance shifts downbay and is more associated with the ETM. In the ETM, production of *Eurytemora* is not food limited suggesting that this copepod is well suited for conditions in the ETM (Lloyd, 2006). The elevated zooplankton concentrations and enhanced overlap with striped bass larvae probably result from enhanced detrital-based production of zooplankton (Heinle and Flemer, 1975; Roman, 1984), as well as increased aggregation and retention in the ETM (Roman et al., 2001; Kimmel and Roman, 2004).

In 2003, when conditions were highly favorable, most striped bass larvae occurred in the ETM and feeding success, apparent survival, and YOY recruitment strength were all high. A high percentage (91%) of larvae in 2003 were feeding successfully compared to the percentage (54%) feeding successfully in 2001 (Figure

3-9). For first-feeding larvae, the difference in feeding success was even more striking: 2003 (91%), 2001 (35%).

The relative importance of the ETM appears to vary between years but it is always a prominent physical feature in the upper Bay nursery and appears to play a prominent role in striped bass recruitment variability. Most upper Bay spawning by striped bass occurs within 10-30 km of the ETM and prevailing currents favor transport to and retention within the ETM (North and Houde, 2001, 2006). Other anadromous and estuarine fishes depend on ETM/salt front structure and dynamics to support reproduction. Atlantic tomcod *Microgadus tomcod* larvae in the Hudson River occur in association with the salt front and their location is controlled by freshwater flow (Dew and Hecht, 1994). Larval rainbow smelt is abundant in the St. Lawrence River's ETM (Dodson et al., 1989) and maintains position there using active tidally-timed vertical migration (Laprise and Dodson, 1989). In many respects, ETMs bear similarities to other small- and mesoscale fronts in marine systems, such as the shelf-break front in the Skagerrak and the Kattegat, North Sea, where cod *Gadus morhua* and other gadoid larvae are aggregated (Munk et al., 1995). The association of larval cod and other gadoids with this front is a general and recurrent phenomenon, dependent on predictable spawning habits and physical aggregation of larvae at the front.

Distribution patterns of egg and larval stages of striped bass in tributaries of Chesapeake Bay, suggest that the dynamics of the ETM and salt front also play a role in controlling recruitment of striped bass in those sub-estuaries. A larval mark-recapture study in the Patuxent River yielded numerous recaptures of larvae released

at or up estuary of the salt front but none for larvae released below the salt front, suggesting advective loss of these larvae (Secor et al., 1995). Research in the Potomac River reported that striped bass eggs usually were collected upriver from peak concentrations of yolk-sac and feeding-stage larvae; the yolk-sac and feeding-stage larvae centers of abundance usually were closer to the salt front and generally exhibited a high degree of spatial overlap (Setzler et al., 1981). The distribution of eggs and larvae in the Potomac suggests that eggs are transported down-estuary, and yolk-sac and feeding larvae are aggregated and retained within and above the salt front and ETM. In the Nanticoke River in 1992 and 1993, Houde and Secor (1996) reported highest concentrations of naturally-produced and hatchery-source striped bass larvae immediately above the ETM/salt front. The Nanticoke results resembled my observations in the upper Bay. In the Nanticoke, recruitment was >2 times higher in 1993 when the salt front and ETM were displaced 8-11 km further downriver under conditions of relatively high freshwater flow.

Spatial and Inter-annual Differences in Diet Composition

Differences in the abundances and spatial distribution of *Eurytemora* and *Bosmina* under variable freshwater flow conditions likely contribute to feeding success and taxon-specific feeding conditions at locations where larval striped bass occur. In the two wet years (1996 and 2003), peak concentrations of larval striped bass occurred within and just above the ETM and salt front (Figure 3-13). In 1996, *Bosmina* concentrations were high just above and extending downbay to the salt front

and ETM and concentrations of *Eurytemora* were elevated further down-estuary within the ETM center (Figure 3-12). Most striped bass larvae fed successfully in 2003. Feeding success on *Bosmina* was enhanced above the ETM and salt front at lower salinities and turbidities, while feeding on *Eurytemora* was enhanced at higher salinities within the salt front and ETM (Table 3-3). In the Patuxent River, Campfield (2005) reported increased consumption of *Bosmina* by striped bass larvae in freshwater above the salt front and ETM, while larvae below the salt front consumed mostly calanoid copepods, including *Eurytemora* and *Acartia*. Similarly, consumption of cladocera, most likely *Bosmina*, was highest upriver of the salt front in the Nanticoke River (Houde and Secor, 1996). In the Hudson River, consumption of *Bosmina* by striped bass larvae was highest near the freshwater-saltwater interface (Limburg et al., 1997).

The higher concentrations and seasonal variability of *Eurytemora* in the upper Bay indicates that it is more important than *Bosmina* in determining inter-annual differences in overall prey availability. For example, in 1996 the extraordinary prey concentrations ($250,000 \text{ m}^{-3}$) that promoted high larval survival of striped bass were almost exclusively *Eurytemora* (Figure 3-12). Concentrations of *Bosmina* rarely exceed 8000 m^{-3} in upper Chesapeake Bay, but *Bosmina* concentrations in the Hudson River may exceed $100,000 \text{ individuals m}^{-3}$ and may be the primary prey supporting larval striped bass growth and survival (Limburg et al., 1997). In the Hudson, striped bass larvae produced coincident with the spring bloom of *Bosmina freyi* are at an energetic advantage compared to larvae produced before the spring bloom. In the Chesapeake, *Bosmina* may contribute significantly to enhanced feeding success during

strong recruitment years as indicated by the high proportion of striped bass larvae consuming *Bosmina* in 2003 (50%) when recruitment was very high compared to 2001 (21%) when recruitment was lower (Figure 3-4).

Relatively weak effects of turbidity on feeding by striped bass larvae were detected in 2003. Total prey consumption by small larvae was higher at lower turbidities and above the ETM center. Shoji et al. (2005) did not detect a turbidity effect on feeding by larval white perch in the upper Bay ETM, and concluded that prey concentration alone was the best predictor of white perch larval feeding success. A negative relationship I observed between *Bosmina* consumption and turbidity in 2003 (Table 3-3) probably resulted because *Bosmina* concentrations were higher upbay of the ETM where turbidity levels are reduced.

Observed patterns in feeding by larval striped bass are consistent with two previous studies on zooplankton prey and larval striped bass and white perch distribution in the upper Bay. Large-scale (>10 km) distribution patterns of striped bass larvae were explained by both *E. affinis* and *B. longirostris* (North and Houde, 2003). In contrast, at small scales in the vertical dimension (< 10 m) at a fixed station in the upper Bay ETM, distribution of larval striped bass was concordant with *Eurytemora* but not *Bosmina* (North and Houde, 2006), possibly because *Bosmina* was not abundant at the fixed station in the ETM. Based on the fixed-station analysis, North and Houde (2006) hypothesized that larval striped bass track *Eurytemora* prey within the ETM

Annual differences in feeding success by larval striped bass were not attributable to differences in turbidity levels. Larvae fed more successfully in 2003

than in 2001 despite higher turbidity levels in 2003. Total suspended solid levels were lower than the 200-500 mgL⁻¹ found to inhibit feeding on copepods by striped bass larvae in laboratory experiments (Breitburg 1988). Peak concentration within the ETM was 80 mg L⁻¹ in 2001 compared to 116 mg L⁻¹ in 2003. These turbidity levels were lower than turbidity treatments in a laboratory experiment that found no effects on growth or survival (Chesney, 1989). Chesney concluded that turbidity levels in nursery areas generally are not high enough to affect larval reactive distance (typically < 10 mm) and prey encounter rates, but the effect of turbidity on light level might affect feeding success of striped bass larvae.

Striped bass larvae are able to feed to an extent in very low light or no light. Research on feeding by larval white perch, a congener of striped bass in the upper Bay ETM reported that feeding on *Eurytemora* and larval growth rates were not negatively affected by high turbidities or low light levels (Shoji et al., 2005). However, the authors concluded that light levels in the upper Bay ETM usually fall below levels required for striped bass larvae to feed visually (0.008 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) (MacIntosh and Duston, 2007). My results and results from laboratory experiments (Chesney, 1989) confirm that striped bass larvae are well adapted to live in the highly turbid and low light conditions in the ETM of upper Chesapeake Bay as Mansueti (1961) suggested many years ago. However, successful visual feeding may at times be compromised and mechano- or chemo-sensory feeding modes are probable as Chesney (1989) hypothesized.

Factors controlling prey availability to larval striped bass potentially can control year-class strength. Probable mechanisms underlying the observed patterns in

recruitment include direct and interacting effects of prey production and availability, estuarine circulation, and larval behavior. Strong environmental-recruitment correlations were previously reported for Chesapeake Bay striped bass and presumably these also were related to differences in prey availability among years (Boynton, 1976; Summers and Rose, 1987). Individual-based modeling (IBM) of Potomac River striped bass indicated that differences in prey availability alone during the larval stage could account for 10-fold variability in recruitment to the age-0 juvenile stage (Cowan et al., 1993). Additionally, Cowan et al. (1993) concluded that large eggs, produced by older/larger females could contribute positively to recruitment success. That IBM model was developed during a time when the age and size structure of Atlantic coast striped bass was shifted toward younger and smaller spawners. Since recovery of the stock, environmental controllers of prey available to larvae may have increased in importance.

The findings in my study should be considered in management of the striped bass fishery, because they include a strong recruitment-environmental relationship that is supported by a mechanistic understanding of the process that supports production of YOY striped bass. A working group of scientists recently evaluated the feasibility of incorporating recruitment-process research into fishery stock assessments (ICES, 2001). The report discusses characteristics of stocks that are good candidates for incorporation of recruitment-process information. In general, stocks should demonstrate both a strong environmental-recruitment relationship and a dominance in the fishery by strong year classes. Chesapeake Bay striped bass would be worthy of consideration based on these criteria.

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Table 3-1. Number of Tucker trawl samples, mean concentration (no. m⁻³) and standard deviation (S.D.) of striped bass eggs, yolk-sac larvae, and feeding-stage larvae in upper Chesapeake Bay in 2001, 2003, 2003.

Year	No. Samples	Eggs	S.D.	Yolk-sac larvae	S.D.	Feeding-stage larvae	S.D.
2001	130	0.84	1.38	0.047	0.093	0.02	0.05
2002	126	0.68	2.23	0.03	0.06	0.001	0.01
2003	65	0.05	0.11	0.90	1.67	3.70	6.93

Table 3-2. Data sources used for analyses on spatial and temporal mesozooplankton variability. The time periods chosen for spatial analyses were selected to coincide with available ichthyoplankton survey data. Time periods chosen for the temporal analyses represent the longest consecutive period when there were no major changes in sampling in the upper Bay.

Data Sources	Temporal Period	Spatial Coverage	Sampling Method
Spatial Analyses			
Chesapeake Bay Program mesozooplankton monitoring	April and May 1996, 1998,1999, 2001,2002	Stations CB2.1, CB 2.2, CB3.3C, CB4.3C	202uM bongo net oblique tows
NSF BITMAX project	May 2003	50km at 5-10 km intervals	Multifrequency acoustic backscatter, TAPS
Temporal Analyses			
Chesapeake Bay Program mesozooplankton monitoring	Monthly March through May, twice (only CB2.1 and CB2.2) during May 1993-2002	Stations CB2.1, CB2.2, CB3.3C	202uM bongo net oblique tows

Table 3-3. Results of ANCOVA and GLM analysis on determinants of feeding success in striped bass larvae in upper Chesapeake Bay during May for the years 2001, 2002, and 2003. Tests of spatial effects were conducted separately for larvae < 7.5 mm and ≥ 7.5 mm standard length. p-values and n.s. are listed in table for significant and non-significant (n.s.) effects respectively. Coefficient values are shown in parentheses for selected significant effects.

Size and Annual Effects	Total prey consumed	Eurytemora consumed	Bosmina consumed			
Larval size (SL)	<0.0001 (+0.36)	-	-			
Year * Larval Size	<0.01	-	-			
Year	<0.001	<0.1	<0.0001			
		<u>< 7.5 mmm</u>			<u>>= 7.5 mmm</u>	
Spatial / Abiotic effects*	Total prey consumed	Eurytemora consumed	Bosmina consumed	total prey consumed	Eurytemora consumed	Bosmina consumed
2001						
Distance Downbay (km)	n.s.	n.s.	-	n.s.	<0.05 (+0.03)	-
Salinity	n.s.	n.s.	-	n.s.	n.s.	-
Turbidity	n.s.	n.s.	-	n.s.	n.s.	-
2003						
Distance Downbay (km)	<0.05(-0.02)	n.s.	<0.0001(-0.05)	n.s.	<0.05(+0.03)	<0.0001(-0.06)
Salinity	<0.05(-0.04)	n.s.	<0.01(-0.06)	n.s.	<0.1(+0.04)	<0.0001(-0.08)
Turbidity	<0.05(-0.03)	n.s.	<0.01(-0.05)	n.s.	n.s.	<0.05(-0.03)

Table 3-4. Geometric mean concentration (no. m⁻³) of mesozooplankton prey at all monitoring stations in the upper Bay , exclusively where striped bass larvae occurred, and at the location where the peak concentration of larvae occurred during mid April through May in dry years 1999 and 2002, normal freshwater discharge years 1998 and 2001, and wet years 1996 and 2003.

Year	Concentration upper Bay	Concentration overlapping with larvae	Concentration at center of larval abundance
Low recruitments			
1999	1672	N.A.	N.A.
2002	531	606	1935
Average recruitments			
1998	1299	1090	1802
2001	7422	2296	275
Strong recruitments			
1996	7416	14404	269263
2003	22873	15877	286160

Table 3-5. Results of correlation analysis between age-0 juvenile striped bass recruitment (CPUE) and concentration of mesozooplankton prey (no. m⁻³) at all upper Bay locations , exclusively where striped bass larvae occurred, and at the location where most striped bass larvae occurred. The analysis period includes the years 1996 through 2003 excluding 1997 and 2000 when data was unavailable. Significant relationships indicated as bold text.

	Zooplankton all areas in upper Bay	Zooplankton overlapping with larvae	Zooplankton at center of larval abundance
Slope coefficient	0.0005	0.0007	0.00003
adjusted R ²	0.34	0.79	0.74
p-value	0.13	0.03	0.04

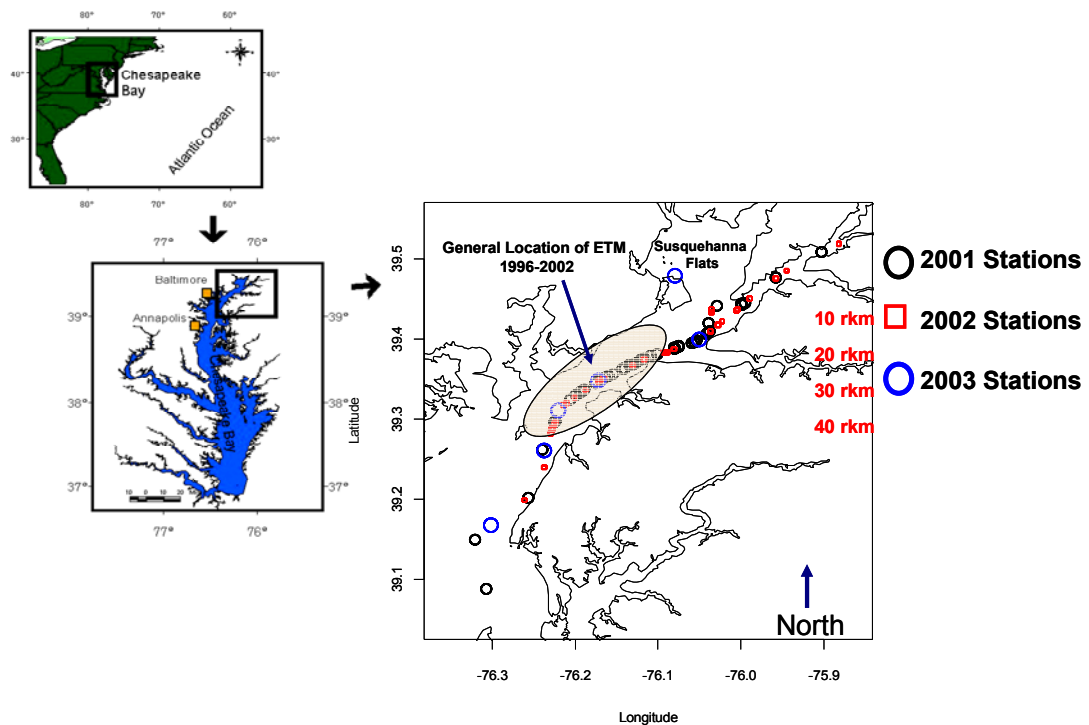


Figure 3-1. Research location and ichthyoplankton sampling stations in Chesapeake Bay during three NSF-funded projects including one during 1995-2000, a second during 1998 and 1999, and a third during 2001-2003. Tucker trawl axial survey stations conducted during cruises in May are shown on map. Stations from 2001-2003 are shown on the map but locations of stations in other years were similar and most were located within 5km of the ETM (ellipse area).

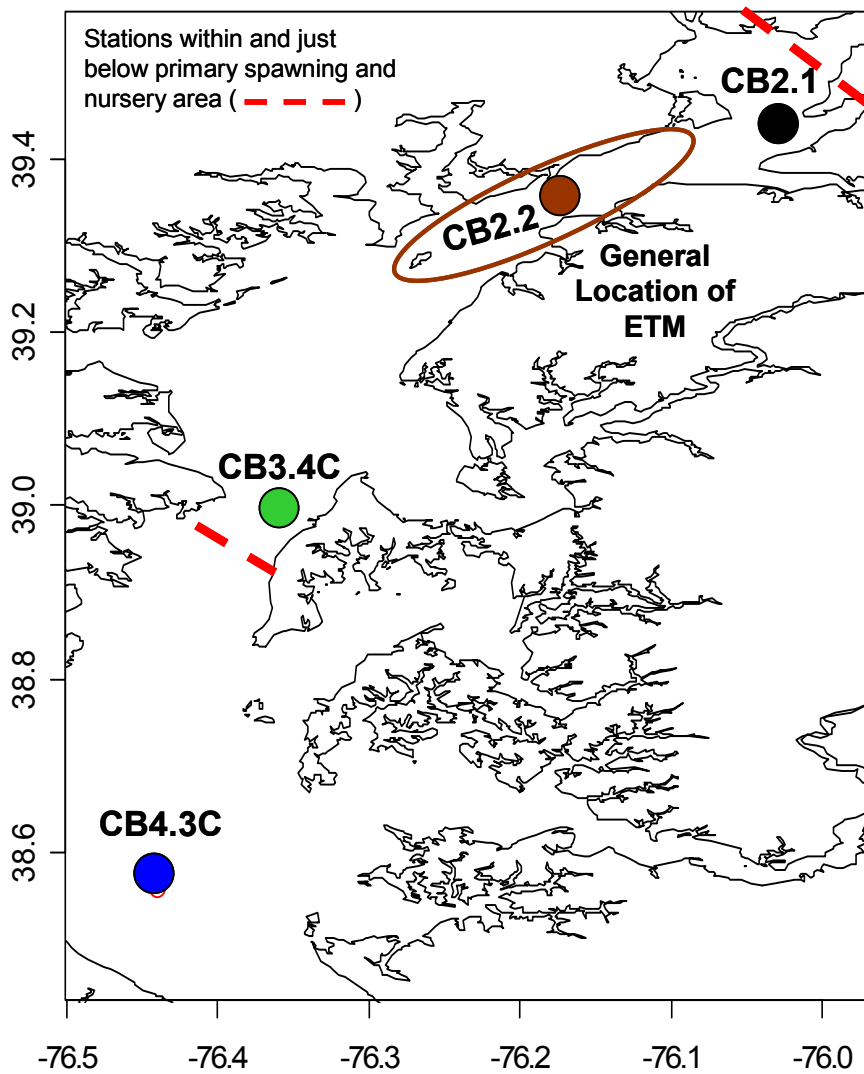


Figure 3-2. Locations of Chesapeake Bay Program mesozooplankton monitoring stations used in this research.

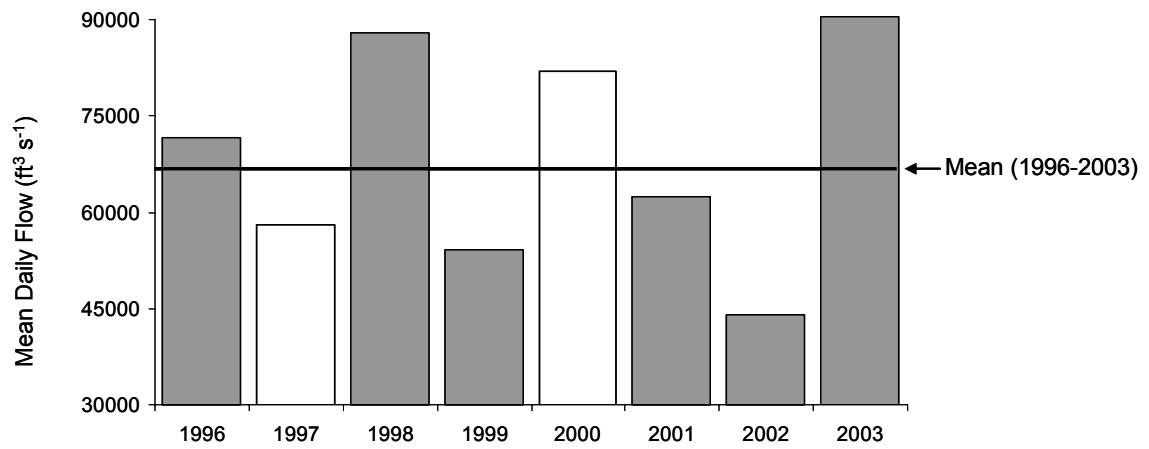


Figure 3-3. Mean daily Susquehanna river discharge during March and April for the years 1996 through 2003 at USGS Conowingo Dam station. Shaded bars indicate years in this study.

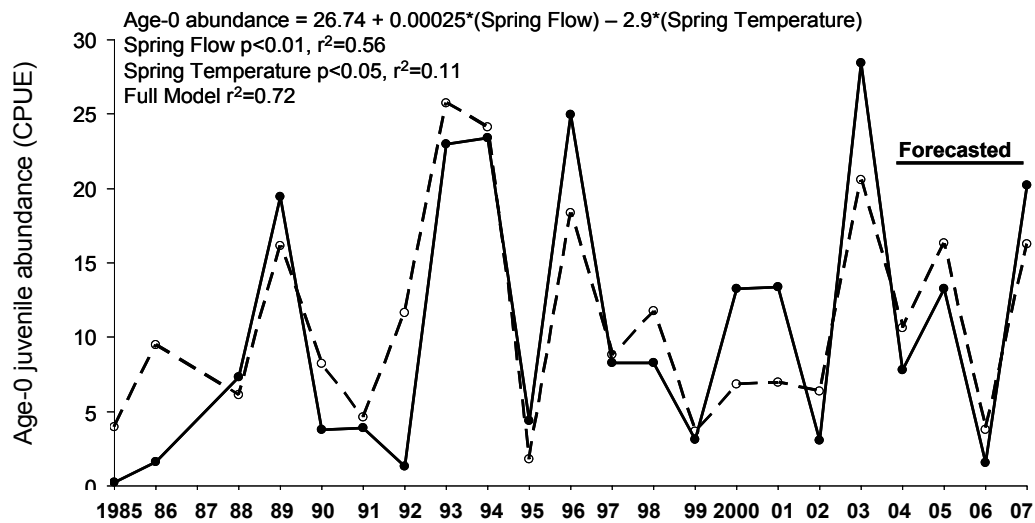


Figure 3-4. Observed, predicted, and forecasted age-0 juvenile abundance in upper Chesapeake Bay. The solid line indicates age-0 abundance observed in the MD DNR recruitment seine survey. The dashed line indicates the predicted values of age-0 abundance for the period 1985 through 2003 and forecasted abundance for the most recent 4 years.

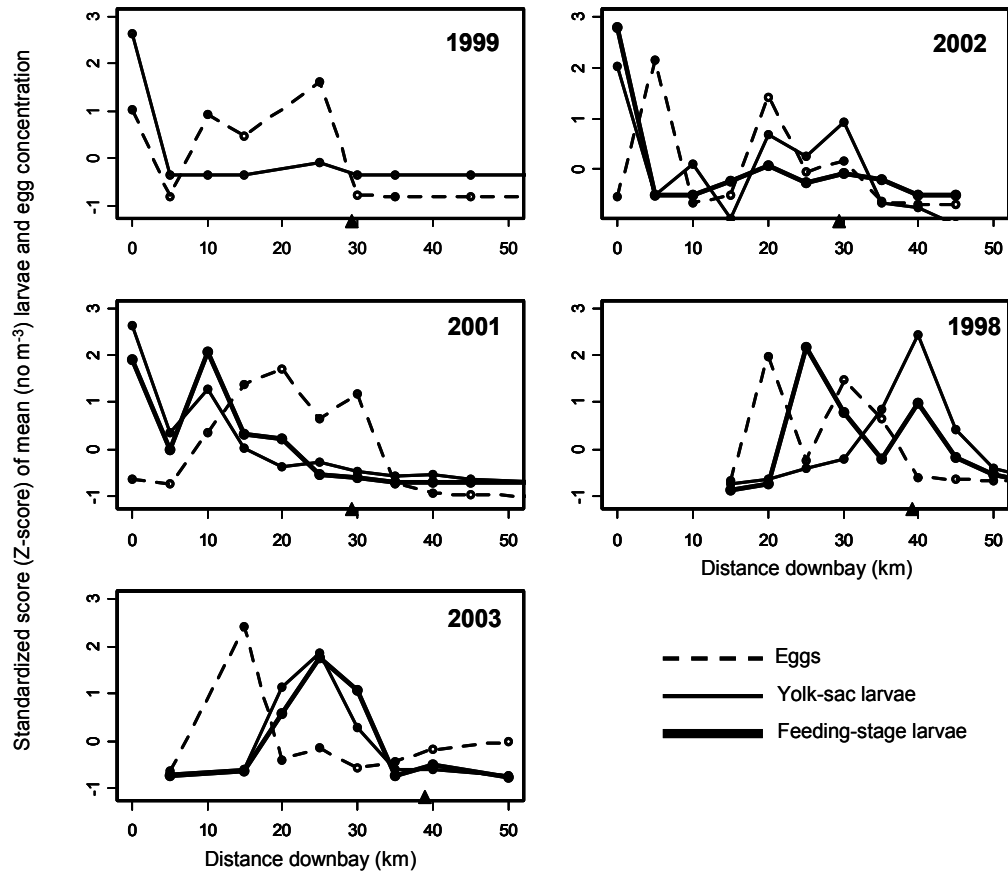


Figure 3-5. Inter-annual variability in the average distribution of striped bass eggs and larvae along the main axis of upper Chesapeake Bay during April and May in two dry years (1999 and 2002), an average freshwater discharge year (2001), and two wet years (1998 and 2003). ETM midpoint is indicated by the triangle symbol on x-axis.

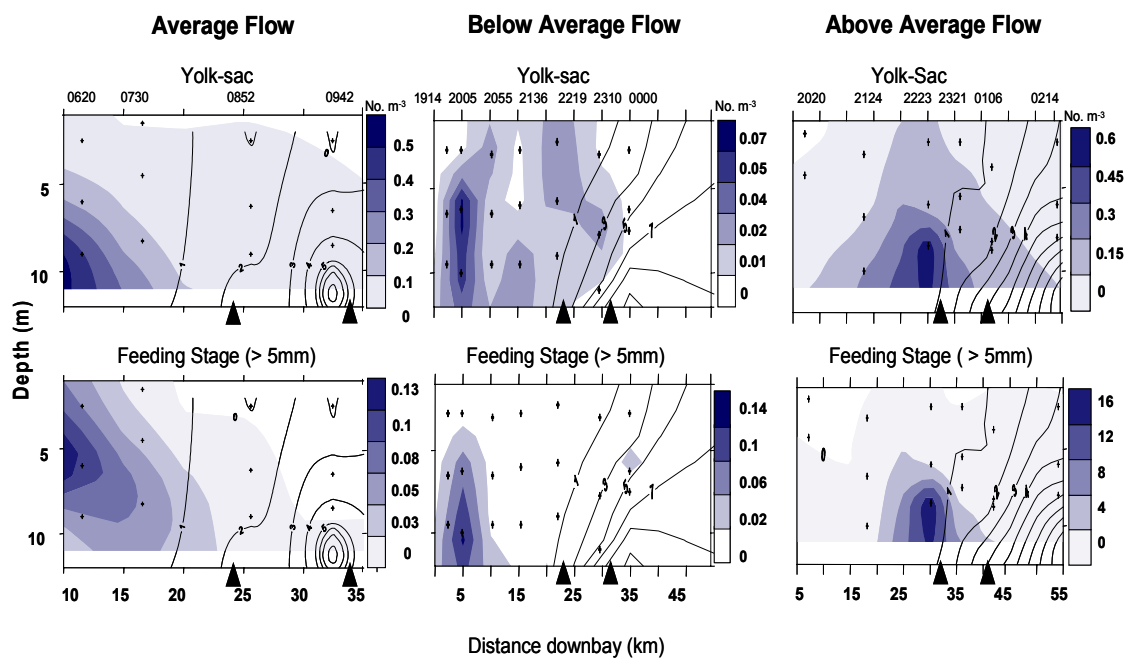


Figure 3-6. Inter-annual variability in the distribution of striped bass eggs and larvae (no. m^{-3}) during surveys in 2001, 2002, and 2003 when March and April springtime discharge levels were average, below average, and above average, respectively. Range of ETM position in each year is indicated by black symbols on x axis. Black points indicate mid-point depth of tows.

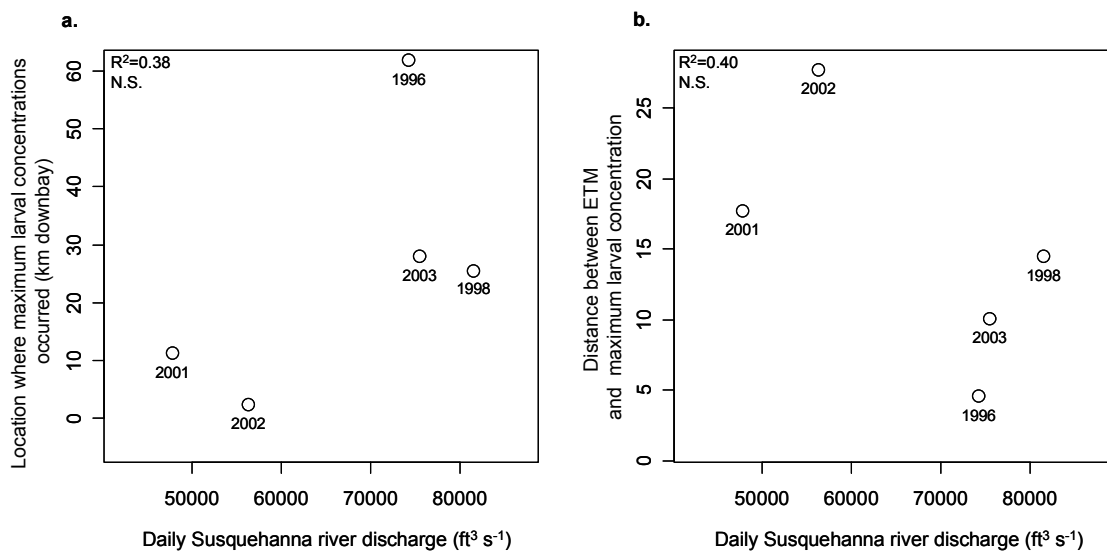


Figure 3-7. Effect of spring (March through May) freshwater discharge on striped bass feeding-stage larvae distribution a) along the main channel in upper Chesapeake Bay and b) relative to the ETM.

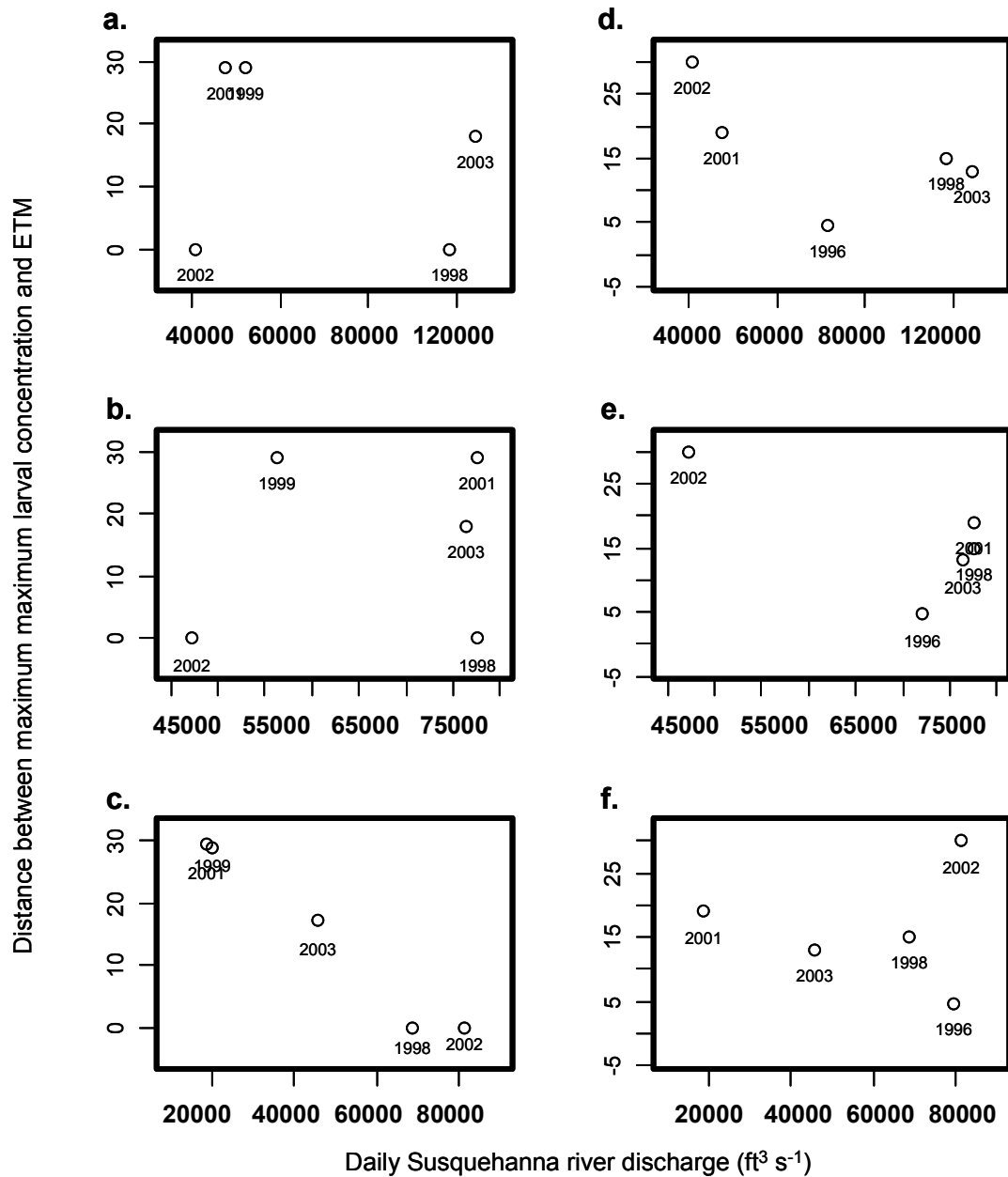


Figure 3-8. Effect of freshwater discharge during different months on striped bass larvae location and association with the ETM. Yolk-sac larvae location during May in response to flows during a) March, b) April, and c) May and the feeding-stage larvae location during May in response to flows during d) March, e) April, and f) May for six years in upper Chesapeake Bay during.

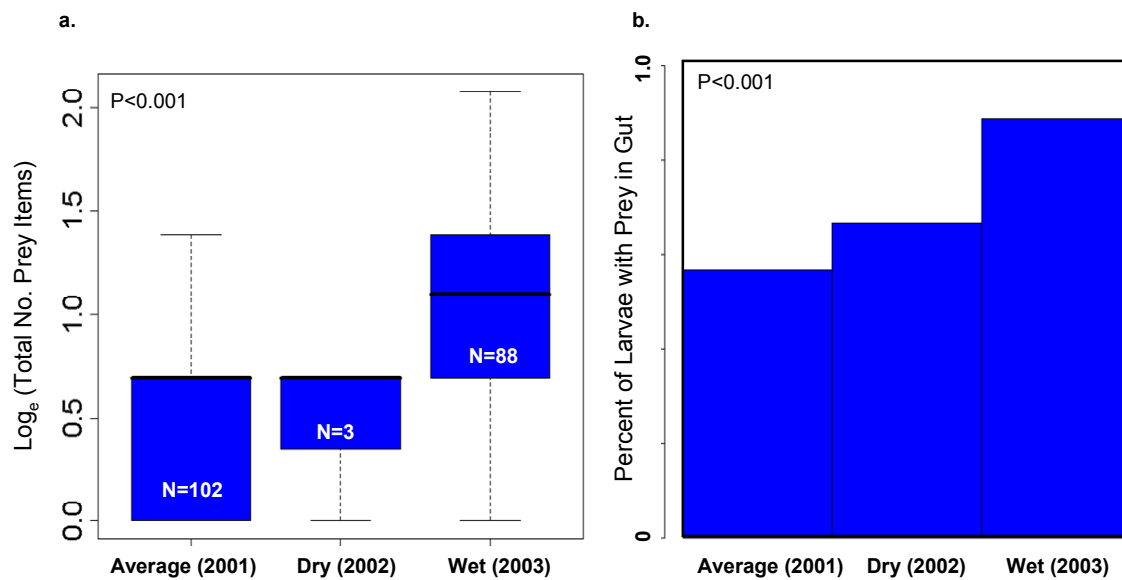


Figure 3-9. Feeding success of striped bass larvae based on a) number of prey items in larval guts and b) percentage of larvae with prey in guts in upper Chesapeake Bay, 2001, 2002, and 2003.

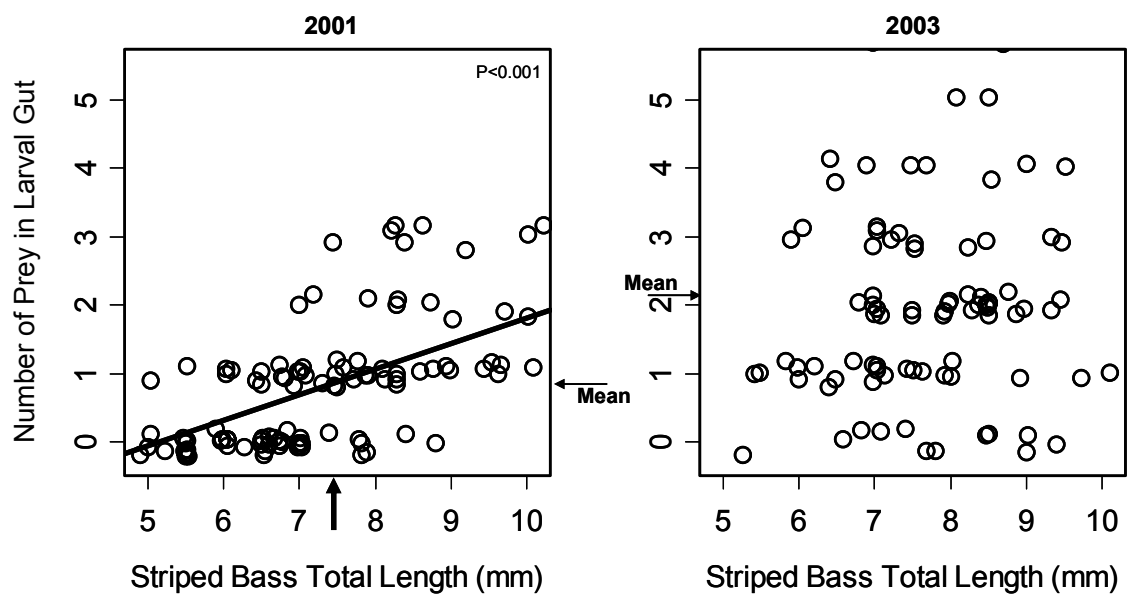


Figure 3-10. Feeding success by size of striped bass larvae in 2001 and 2003 in upper Chesapeake Bay.

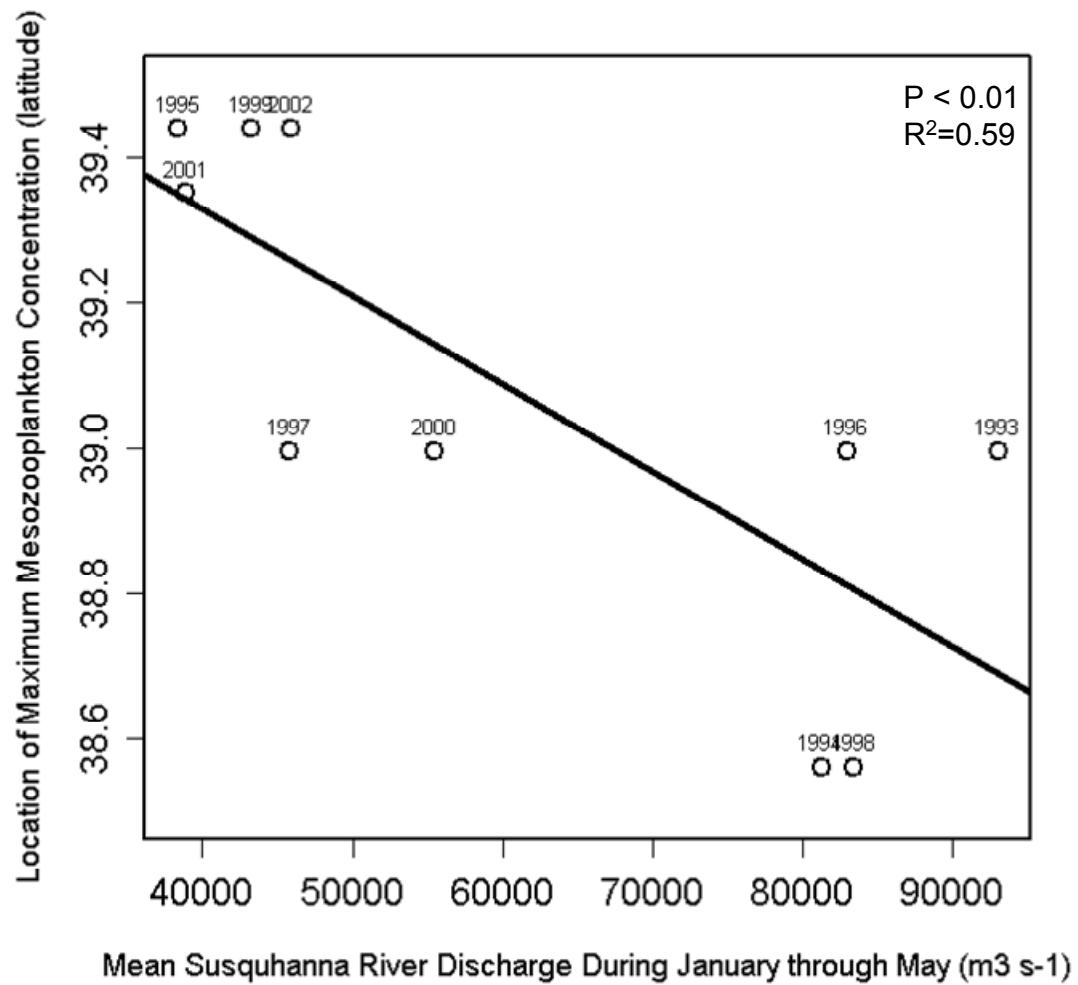


Figure 3-11. Effect of annual hydrological conditions on broad patterns in distribution of dominant mesozooplankton including *Eurytemora affinis*, *Bosmina longirostris*, and *Acartia tonsa* distribution for 9 years in upper Chesapeake Bay.

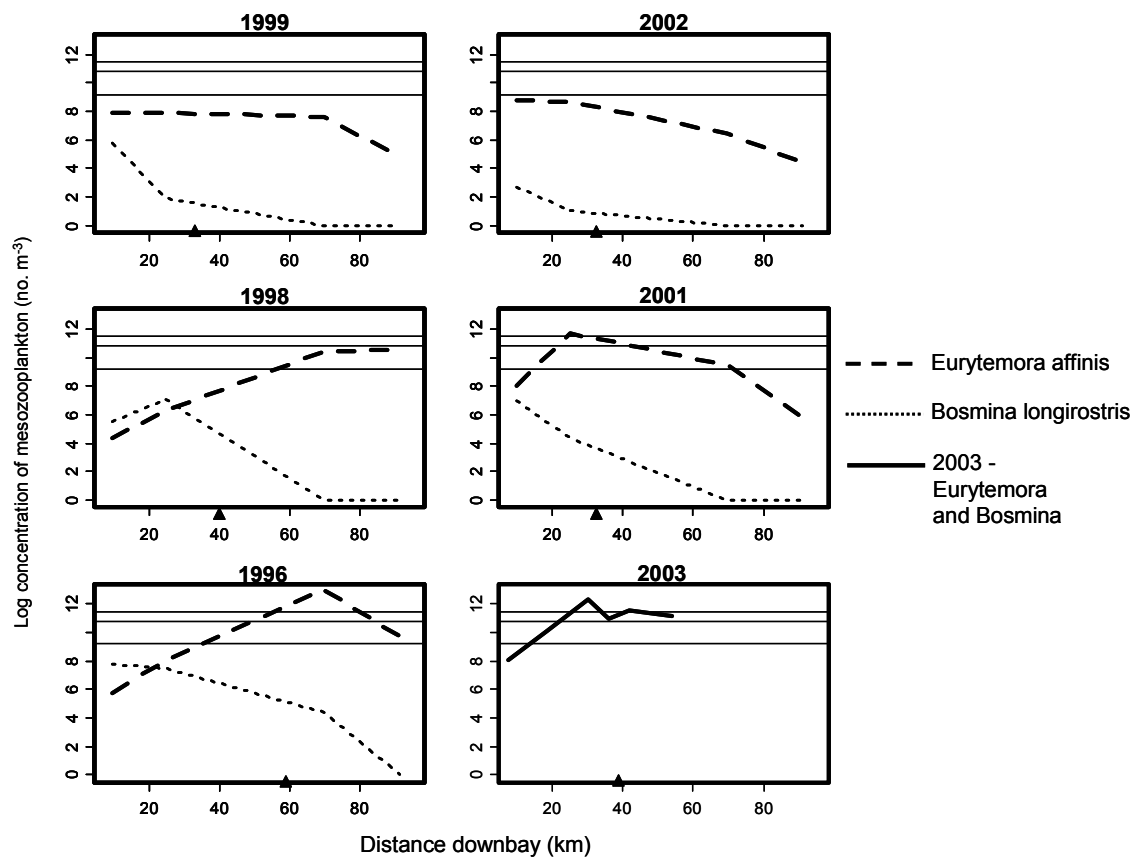


Figure 3-12. Spatial distribution of the calanoid copepod *Eurytemora affinis* and the cladoceran *Bosmina longirostris* in upper Chesapeake Bay during April and May when spring freshwater flows were low (1999 and 2002), when freshwater flows were average (2001), and when freshwater flows were above average (1998, 1996, and 2003). Horizontal lines indicate three different estimates of minimum required prey levels for favorable survival and growth of striped bass larvae. ETM midpoint indicated by the triangle symbol on x-axis.

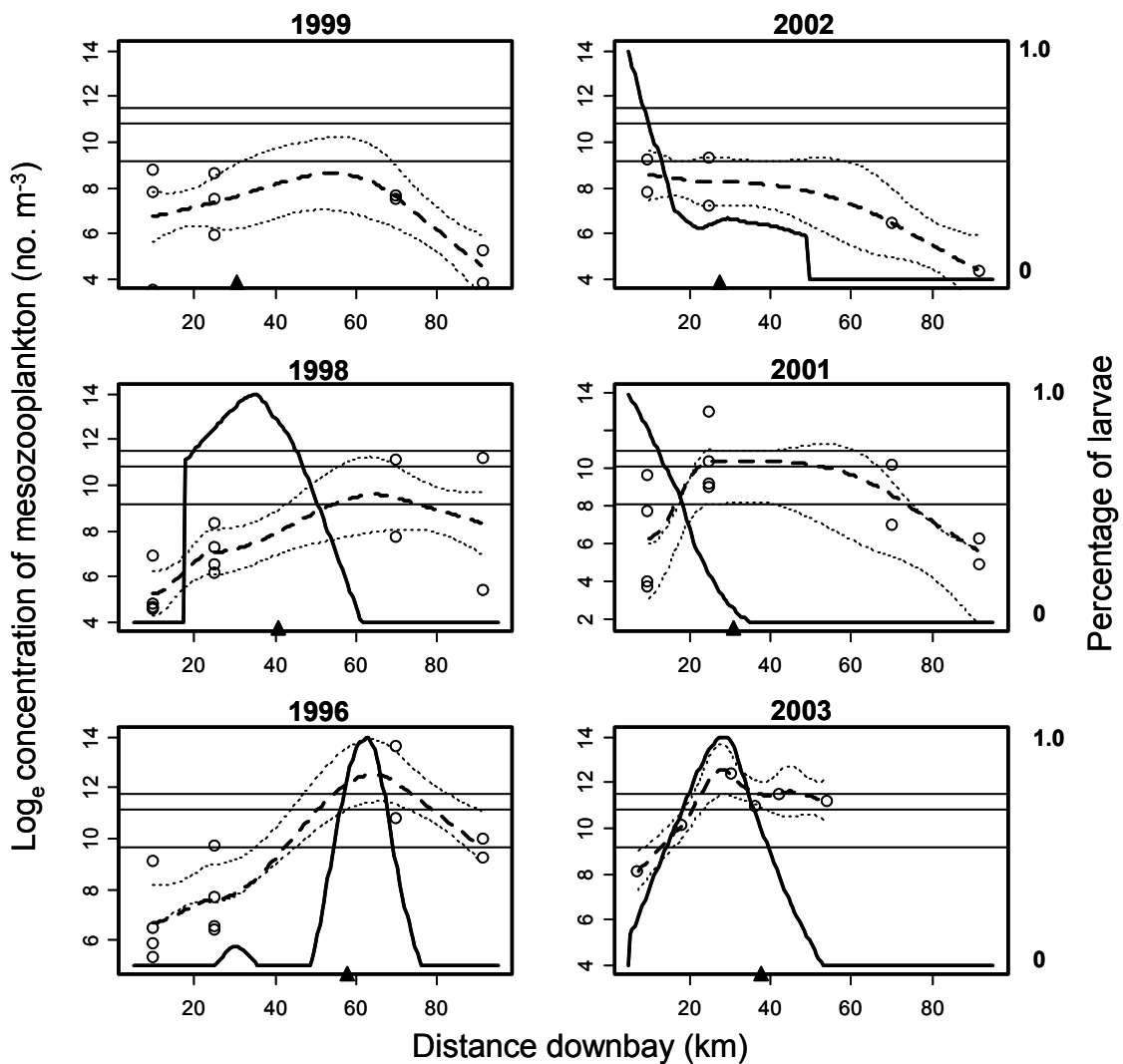


Figure 3-13. Spatial match-mismatch of striped bass feeding-stage larvae and total zooplankton prey in upper Chesapeake Bay when spring freshwater flows were low (1999 and 2002), when freshwater flows were average (2001), and when freshwater flows were above average (1998, 1996, and 2003). Loess curves were fit to concentrations of zooplankton (open symbols and dashed line, dashed standard errors) and percentage of larvae (solid line). Horizontal lines indicate three different estimates of minimum required prey levels for favorable survival and growth of striped bass larvae. ETM midpoint is indicated by the triangle symbol on x-axis.

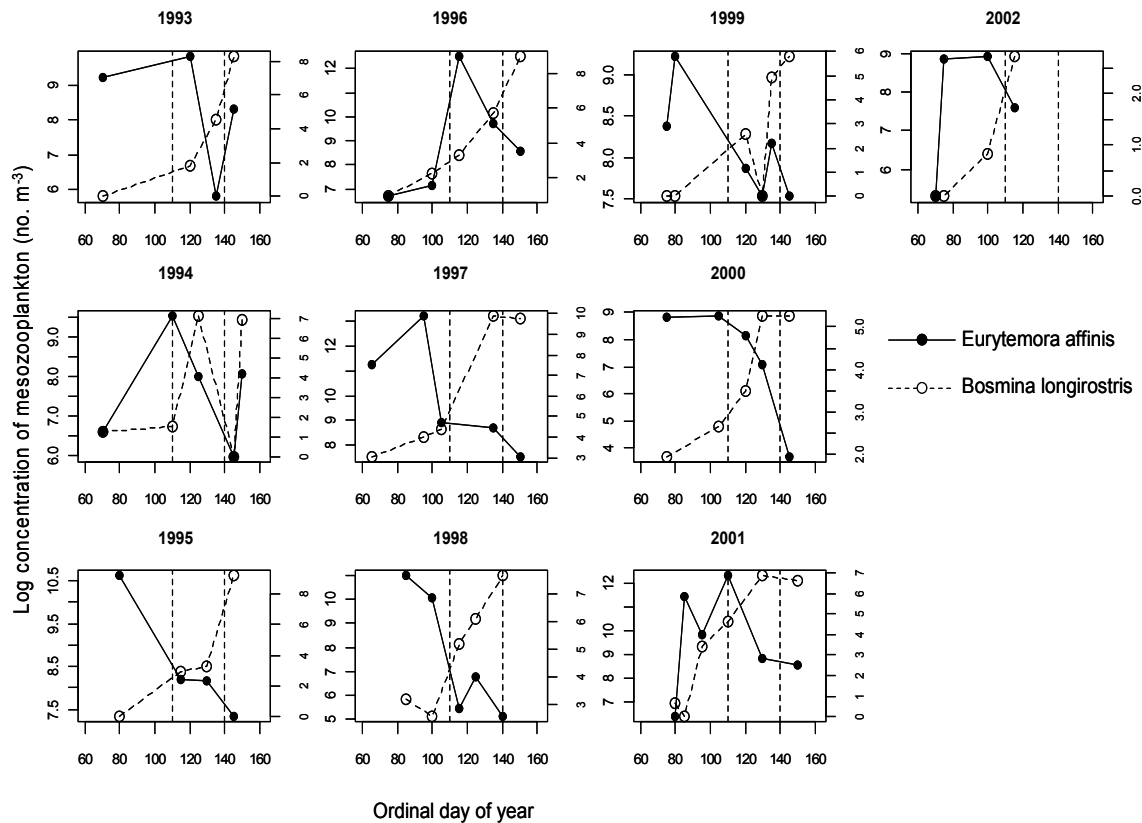


Figure 3-14. Temporal patterns in dominant mesozooplankton prey of striped bass larvae in upper Chesapeake Bay. Points and lines represent the average concentrations (log no. m⁻³) of mesozooplankton pooled across 3 monitoring stations for a given ordinal day. Dashed vertical lines indicate the period when most striped bass larvae occur in upper Chesapeake Bay based on previous egg and ichthyoplankton surveys.

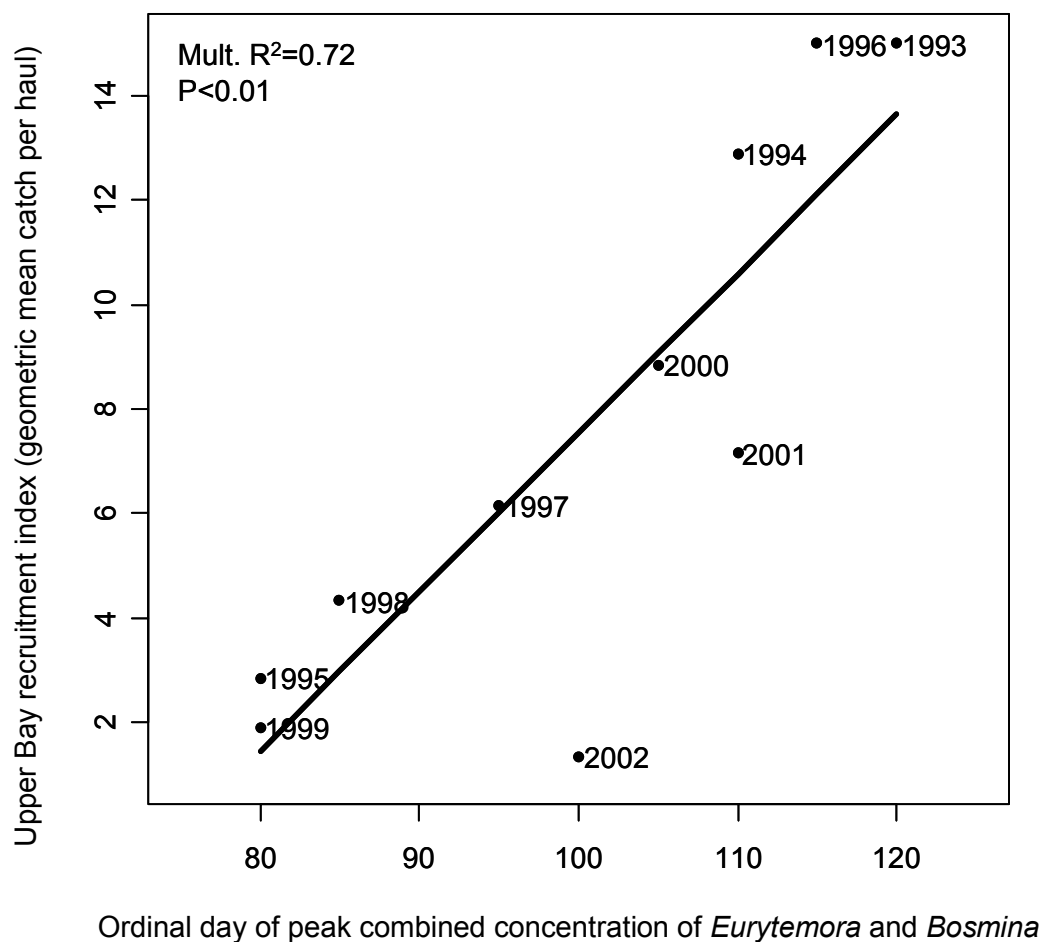


Figure 3-15. Temporal match-mismatch with respect to striped bass YOY recruitment in upper Chesapeake Bay. Relationship between the timing of peak larval striped bass prey, including *Eurytemora affinis* and *Bosmina longirostris* and recruitment of age-0 juvenile striped bass.

CHAPTER FOUR

Larval Striped Bass: Growth and Recruitment Variability in the ETM of Upper Chesapeake Bay

INTRODUCTION

The importance of recruitment variability in determining year-class strength of marine fishes was recognized early in the 20th century (Hjort, 1914) and fostered “recruitment thinking” (Solemdal and Sinclair, 1989) among fishery scientists. Recruitment variability in fish populations can exceed 100-fold and 10-fold variability is common. A lack of understanding of processes and mechanisms supporting recruitment and its associated variability motivated major research programs in the last decades of the 20th century that focused on early-life survival in fish and recruitment variability. The underlying mechanisms controlling recruitment variability are usually complex, and uncertain explanations of possible causes are more the norm rather than the exception. Not surprisingly, the role of early-life stages in generating recruitment variability remains a prolific research topic due, in part, to the current crises facing sustainability of many fisheries and other marine resources (Baum et al., 2003; Myers and Worm, 2003).

Variability in recruitment frequently is the consequence of variability in survival of the abundant egg and larval stages (Cushing, 1975; Houde, 1989). Variability in early-life survival was hypothesized to be generated by environmental

determinants affecting prey availability and survival of first-feeding larvae (Hjort, 1914; Cushing, 1975). Thus, dominant year classes are formed early in life during the larval stage and the relative strength of a year class in a population may persist for several years (Hjort, 1914). Invoking and testing Hjort's hypothesis prevailed for decades as the major approach to understanding what came to be known as the 'recruitment problem.'

Larval-stage growth is linked to mortality through what Cushing (1975) termed the "single process," i.e., stage-specific mortality linked to growth rates. Small and difficult-to-detect changes in mortality rates can have surprisingly large effects on cumulative early-life mortality and year-class strength (Sissenwine, 1984; Houde, 1989), posing a formidable challenge to scientists conducting research on the recruitment process. Growth and mortality rates both must be accurately and precisely estimated to detect small, but possibly important, variability that can control recruitment level. Accurate and precise growth rate estimates are easier to obtain than are mortality estimates. While recruitment variability may depend more on variability in instantaneous mortality (M) than weight-specific growth (G) (Houde, 1997), cumulative and stage-specific mortality are linked to growth and growth-dependent factors that are correlated with recruitment potentials.

Understanding growth and size variability among individuals and cohorts has become a central theme in recruitment research. Two primary hypotheses have been proposed to explain the positive association between growth, size, and survival including the "bigger is better" (Miller et al., 1988) and stage-duration (= faster is better) hypotheses (Houde, 1987; Anderson, 1988; Leggett and Deblois, 1994). As

examples, fast growth and larger size-at-age were selected for in Atlantic cod larvae (Meekan and Fortier, 1996); larval rainbow smelt (*Osmerus mordax*) in the St. Lawrence River estuary and ETM grew faster than larvae in the average population (Sirois and Dodson, 2000); and, larger size damselfish *Neopomacentrus filamentosus* were more likely to survive the planktonic stage before settling on a coral reef (Vigliola and Meekan, 2002). The general consensus is that larger individuals (Miller et al., 1988) and individuals growing faster (Houde, 1987; Pepin, 1989) are less vulnerable to predation (Bailey and Houde, 1989; Leggett and DeBlois, 1994) and other sources of size- and stage-specific mortality, and thus experience reduced cumulative mortalities.

Historically, research on striped bass recruitment variability in Chesapeake Bay has focused on some combination of larval feeding success, growth rates, and size-at-age differences based on cohort analysis within and between years (Beaven and Mihursky, 1980; Logan, 1985; Setzler-Hamilton et al., 1987; Rutherford et al., 1997). Most of the historical research indirectly or directly evaluated links between prey availability, growth, and survival (Ulanowicz and Polgar, 1980; Eldridge et al., 1982; Logan, 1985; Setzler-Hamilton et al., 1987; Tsai, 1991; Cowan et al., 1993; Rutherford and Houde, 1995; Secor and Houde, 1995; North and Houde, 2003). Considerable progress was made toward understanding the coarse controls over recruitment in Chesapeake Bay striped bass. However, the earlier research either focused on feeding and growth in a single year or on years with little contrast in recruitment strength. Finally, most previous research did not consider biophysical controls over larval distribution, growth, and survival. My research (Chapter 3) and

other recent evidence indicate that larvae associated with the estuarine turbidity maximum (ETM) in strong recruitment years experience enhanced feeding success and apparent survival (North and Houde, 2006).

The overarching goal of this chapter is to evaluate growth of striped bass larvae and its connection to biophysical controls of prey availability that were treated in Chapters 2 and 3. Unlike most of the earlier studies, my research emphasizes identification of processes that lead to inter-annual differences in mean growth resulting from bottom-up effects driven by hydrological and hydrographic variability. A specific objective was to estimate growth rates and growth rate variability of larvae and to evaluate sources of the variability in three years when YOY recruitment varied >15-fold (Chapter 3). I hypothesized that growth rates would be higher in 2003, an exceptional recruitment year, when most larvae were associated with the ETM, compared to growth in 2001, a modest recruitment year, when larvae were not associated with the ETM. A second hypothesis was that annual differences in larval growth and size-at-age would not be detected until the feeding stage when prey concentrations, in addition to abiotic conditions (i.e. temperature or salinity) and maternal investment, are important determinants of larval size and growth. Finally, I hypothesized that surviving larvae would have grown faster and exhibited a larger size-at-age compared to average individuals sampled at earlier dates from the larval population.

MATERIALS AND METHODS

Research Surveys

Research cruises were conducted in the upper Chesapeake Bay (Chapter 3, Figure 3-1). Ichthyoplankton was surveyed during May of 2001, 2002 and 2003. The location of the ETM and salt front were determined from CTD casts in a hydrographic survey conducted on the same day or one day before ichthyoplankton sampling. Based on the hydrographic surveys, selected stations were sampled and gradients in ichthyoplankton abundances were mapped above, within, and below the ETM and salt front (Figure 3-1). A CTD cast also was made at each sampling station immediately prior to ichthyoplankton tows.

Ichthyoplankton was sampled with an opening-closing, 1-m² Tucker trawl with 280-µm meshes in three discrete depths at each station. The volume filtered by a 2-min tow was, on average, 126 m³. Plankton samples were preserved in ethanol. In the laboratory, striped bass eggs and larvae were identified and enumerated and expressed as number of eggs or larvae per cubic meter. Feeding-stage larvae were, on average, collected at fewer than one third of the stations during cruises in 2001 and 2003, and only occurred at 9 of the 126 stations sampled during the 2002 cruise. The larvae were staged (yolk-sac or feeding-stage) and measured to the nearest 0.1 mm. A subsample of striped bass larvae was selected for otolith microstructure analysis from most sites where striped bass were collected. Larvae selected for otolith examination

and analysis of age and growth were chosen to represent the approximate size range collected at a station.

Otolith Analyses

Otoliths were analyzed from striped bass larvae collected in each year (2001-2003), although only 3 individuals of feeding-stage larvae (> 5.5 mm) were available in 2002. Individual larvae were measured to the nearest 0.1mm. Otolith preparation and analysis generally followed procedures in Secor et al. (1991). Larvae were dissected and the pair of sagittal otoliths removed under a stereomicroscope. Otoliths were mounted on glass slides using clear nail polish or crystal acrylate glue.

Three hundred and eighty-six larvae were processed for otolith analysis. Initial inspection of otoliths under a compound microscope revealed imperfections in many of the otolith preparations, resulting in 167 larvae that were usable in analyses (Table 4-1). The otoliths with microstructure imperfections were omitted for a variety of reasons (e.g., anomalies from processing, preservation, and other natural imperfections). Otoliths from the 167 larvae used for analysis were scored from 1 (very good) to 3 (poor) based on my ability to discern increments and overall microstructure. This coding scheme allowed me to evaluate effect of otolith quality on results.

The radius of the nucleus, the width of each daily increment, and radius of the whole otolith were measured using Image J (<http://rsb.info.nih.gov/ij>; developed by Wayne Rasband, National Institutes of Health, Bethesda, MD) image analysis

software to support a back-calculation analysis of age and growth. Daily increment deposition has been validated for striped bass larvae (Secor and Dean, 1989). Most smaller (<50µm) otoliths were approximately circular although larger otoliths had a pronounced region of maximal growth. Increment widths were always measured along the longest growth axis of an otolith. For quality control, the measurements were repeated at least once and otoliths with differences in increment counts or widths that exceeded 10% were either repeated again or eliminated from the analysis. The total number of increments measured beyond the nucleus was used as the daily increment count for ageing analysis.

Temperature affects age of first increment deposition in otoliths of striped bass larvae. The age at first increment deposition was estimated as

$$A_1 = 11.56 - 0.45 T$$

based on (Houde and Morin, 1990), where T is water temperature (°C), the temperature on the day of first increment deposition. Daily water temperatures in the sampling region were predicted from linear interpolation between bi-weekly water temperatures at a depth of 1 meter at a monitoring station that is located where most spawning occurs in the upper Bay (Chesapeake Bay Program Station CB2.1). Mean daily water temperatures on the day of first otolith increment deposition were used to estimate the age at first increment deposition. Ages were estimated as number increments + age of first increment deposition. Somatic growth rate (mm•d⁻¹) was estimated as

$$G_s = \frac{(L_t - L_{t_0})}{Age}$$

Where L_t equals length at capture and $L_{t_0} = 4.0$ mm, the mean standard length (SL) at hatching (Mansueti, 1958).

Back-calculated Lengths

Back-calculation of lengths-at-age was conducted by applying the biological intercept method (Campana and Jones, 1992). The biological intercept was set at 4.0 mm SL, the mean length-at-hatch that has been used in other research on age and growth of striped bass larvae (Rutherford et al., 1997; Limburg et al., 1999). The relationship between somatic and otolith growth was approximately linear for the sizes of larvae used in this study (Figure 4-1). Thus, issues associated with nonlinear proportionality between otolith and somatic growth (Secor and Dean, 1989) were not problematic in my analysis. However, in 2001 the relationship between otolith radius and larval length was not proportional for nine larvae with otolith radii greater than 60 μm . Otolith back-calculation analyses were restricted to otolith radii less than 60 μm and corresponding larval lengths ≤ 8.7 mm due to lack of proportionality between otolith and somatic growth and small sample sizes of larvae with larger otoliths (<3 larvae).

Temperature-Growth Relationship

Growth of striped bass larvae was analyzed with respect to the temperatures experienced by larvae during their life. The mean temperature experienced by larvae was determined from the available temperature data and the back-calculated hatch date and collection date for each larva. Temperature was estimated for each day of life for all larvae analyzed. Mean growth rate and mean temperature experienced between hatching and day of collection were calculated.

Characteristics of Surviving Larvae

To determine if there were size-selective or growth-rate selective survival, the growth rates and sizes of older larval ‘survivors’ were compared with growth rates of the average larval population at an earlier point in time (Meekan and Fortier, 1996). Larvae collected at the beginning (t_1) and end (t_2) of cruises represented the average and surviving larval populations, respectively. The duration over which size and growth-rate selection could operate was 3 days in 2001 but only 2 days in 2003, which were judged to be sufficient to detect differences in survivors, given the high mortality rates of striped bass larvae in Chesapeake Bay (Rutherford et al., 1997) that often exceed 0.2 d^{-1} , resulting in >30% mortality over a 2-day interval. The ‘average’ larvae in my analysis included all individuals sampled on the early cruise date (t_1) that were ≥ 10 dph (days posthatch) and < 14 dph in 2001 and 2003, and whose standard lengths were less than approximately 6.7 mm. The ‘surviving’ cohort included individuals

collected at the end (t_2) of each cruise that were ≥ 15 dph and < 17 dph in 2001 and 2003.

Statistical analysis

Length and age data were fit to linear and exponential models for 2001 and 2003 data. Exponential models provided a better (2003) or similar (2001) fit to the data when compared to linear model fits. Further, regression coefficients (the growth rates) from this study were compared with coefficients from earlier research that were derived from exponential models to describe growth of larval striped bass. In 2001, two outlier data points were removed from the regression analysis and the model refit; removing the outliers did not alter model fits or coefficient estimates appreciably.

Inter-annual differences in mean growth rates were tested by comparing the slopes of the linear regressions of log-transformed standard lengths on ages of larvae. The test for differences was an analysis of covariance (ANCOVA) with age as the covariate and year as the main effect. Growth trajectories of individual larvae were compared between years using repeated-measures analysis of variance (rm ANOVA) to account for the autoregressive covariance structure in successive otolith increment measurements from the same larva. The repeated measures analysis accounted for the lack of independence among observations and increased the sensitivity for detecting differences in growth trajectories (Chambers and Miller, 1995).

RESULTS

Environmental Conditions

Striped bass larvae experienced markedly different hydrographic conditions in the upper Bay in the three years encompassed by this research (Chapters 2 and 3). Freshwater flows from the Susquehanna River during March and April were below the 30-year average in 2001 (19% below 30-year average), were considerably lower in 2002 (42 % below average), and were above the 30-year average in 2003 (17% above). Mean temperatures during the May cruises in the upper Bay also differed considerably among years, with mean values across all stations and depths of 17.7, 17.7, and 16.2 °C in 2001, 2002, and 2003, respectively. Temperatures were consistently above 12 °C by the third week of April in all years (Figure 4-2). The 12 °C temperature is associated with initiation of spawning and also is a lower threshold for survival of most striped bass larvae (Rutherford and Houde, 1995; Secor and Houde, 1995).

Hatch Dates

Peak hatch dates for most larvae analyzed were similar among years (Figure 4-3) and occurred on April 27 and April 30 in May 2001 and 2003, respectively. Only three feeding-stage larvae, representing two hatch dates (April 24 and May 4), were

collected in 2002. Hatch dates for the oldest larvae analyzed occurred on April 19, April 24, and April 25 in 2001, 2002, and 2003, respectively.

Growth Rates

The mean instantaneous growth-in-length rate was 34% higher in 2003 ($.038 \text{ d}^{-1}$) than in 2001 (0.024 d^{-1}). The regression intercept was higher in 2001 (5.19 mm) than in 2003 (4.35 mm) (Figure 4-4). Results of an ANCOVA on 2001 and 2003 log-transformed lengths and estimated ages indicated that growth rate was significantly ($p < 0.001$) higher in 2003, and that the intercept in 2001 was significantly ($p < 0.01$) higher. Inter-annual differences in lengths-at-age were most pronounced for larvae > 15 dph. Most larvae > 15 dph in 2003 were larger than larvae in 2001 of similar age. The lengths-at-age of the three larvae from 2002 fell within the range of observations for 2001 and 2003.

Individual Growth

The relationship between larval standard length and otolith radius was fit reasonably well with linear models in 2001 ($r^2 = 0.71$) and 2003 ($r^2 = 0.81$) (Figure 4-1). Larvae in 2003 and 2001 had similar sized otoliths-at-length and the slope coefficient of the relationship between larval size and otolith size was 0.07 in 2001 and 2003 (Figure 4-1).

Variability in back-calculated lengths-at-age generally increased with larval age in 2001 and 2003 (Figure 4-5). Variability in larval lengths-at-age between otolith increments 5 and 10 (approximate age = 7 to 12 days post hatch) was higher in 2001 than in 2003 but variability was similar for other ages. Higher variability for older and larger striped bass larvae in both years probably resulted from autocorrelation in growth rates between successive days. The disparity in growth between fast and slow growers increased over time.

Median individual growth rates, averaged for the period between hatching and day of capture, were similar in 2001 and 2003 for larvae < 15 dph whereas growth was faster in 2003 for larvae ≥ 15 dph (Figure 4-6). Median growth rates of ≥ 15 dph larvae in 2003 increased from 0.24 mm d^{-1} to 0.28 mm d^{-1} while growth rates in 2001 decreased from 0.26 mm d^{-1} to 0.22 mm d^{-1} (Table 4-2). Larvae attained lengths of 7.5 mm by 15 dph in 2003 but only 6.9 mm in 2001. Mean weight attained at 15 dph, using a length-weight conversion (Limburg et al., 1997), was 1.5 mg in 2001 compared to 2.1 mg in 2003, a 40% difference. Growth of the three larvae analyzed in 2002 was quite variable, and the median growth rate was 0.24 mm d^{-1} .

Growth trajectories of striped bass larvae based on back-calculated larval lengths in 2001 and 2003 were consistent with growth results based on the means of individual rates. Growth trajectories were similar in each year from hatching through 12 dph when larvae were approximately 6.5 mm (Figure 4-7). Growth trajectories diverged after 12 dph. Lengths-at-age in 2003 were conspicuously larger by 14 dph. Results from the rmANOVA on back-calculated lengths-at-age (Figures 4-7) indicated that individuals from 2003 grew significantly faster than individuals from 2001, a

result similar to that in the cross-sectional analysis on average growth rates (Figure 4-4). A significant interaction between dph and Year in the rmANOVA confirmed the significant divergence in lengths-at-age between 2001 and 2003 that occurred at approximately 12 dph ($p < 0.05$ $df = 1195$, Year x Day interaction).

The distribution of otolith increment widths for three different larval age groups of 5, 10, and 15 dph revealed the same trend of increasing growth rates and lengths-at-age for the older 2003 larvae (Figure 4-8). The similar lengths of larvae prior to 13 dph (Figure 4-7), and increasing disparity in otolith increment widths and larval sizes at older ages (Figure 4-8 and Figure 4-7), suggests that inter-annual differences in older larval lengths resulted from accumulating effects of higher growth rates in 2003.

Characteristics of Survivors

Differences in growth trajectories between larval survivors and the average population conformed to the expectation that survivors would have grown faster compared to the average population of larvae. Back-calculated lengths of survivors at 10-13 dph in 2001, a year when recruitment was near average, indicated that they were growing at a faster rate compared to the average population of larvae from 10-13 dph (Figure 4-9a). Surviving larvae in 2001 were growing at 0.30 mm d^{-1} compared to the average population growth rate of 0.21 mm d^{-1} . Surviving larvae in 2001 had attained lengths 0.5 mm longer at 13 dph than the mean length of the average population at that age. Applying a length-weight conversion indicated that weight attained by survivors

at 13 dph in 2001 was 2.0 mg, compared to 1.4 mg in the average population. Survivors at 13 dph were 43% heavier than larvae from the average population. Furthermore, length of survivors in 2001 was accelerating with respect to age, suggesting exponential growth, while growth of the average population appeared to be linear (Figure 4-9a).

Survivors in 2003, a strong recruitment year, also experienced higher growth rates (0.28 mm d^{-1}) and back-calculated lengths were longer compared to growth rates (0.19 mm d^{-1}) and lengths in the average population. The difference in growth was most obvious after 10 dph (Figure 4-9). Surviving larvae in 2003 had attained lengths 0.4 mm longer at 13 dph than the mean length of the the average population. The weight attained by survivors at 13 dph was 1.5 mg, compared to 1.1 mg in the average population. Survivors were 36% heavier than larvae from the average population. Length of survivors in 2003 also was accelerating with respect to age, suggesting exponential growth, while growth of the average population in 2003 appeared to be linear (Figure 4-9).

Environmental Effects on Growth

Temperature had a significant effect on growth of striped bass larvae in 2001 and 2003. Although, larvae collected during May 2001 had experienced a wide range of temperatures (<15 to >19 °C) during their 2-3 weeks of life prior to collection compared to larvae from 2003 (15 to 16 °C). In 2001, there was a positive relationship between mean individual growth rates and mean temperature (Figure 4-

10). Mean growth rate of ≥ 15 dph larvae in 2001 was approximately 0.19 mm d^{-1} at 15°C and increased to $>0.28 \text{ mm d}^{-1}$ at $>17^\circ\text{C}$. The positive effect of temperature was significant ($p < 0.05$) for the youngest (< 15 dph) and oldest (≥ 15 dph) ages. In May 2003, striped bass larvae had experienced only a narrow temperature range (15 to 16°C), but a significant ($p < 0.05$), positive effect on growth was detected for the youngest and oldest larvae (Figure 4-10).

DISCUSSION

A strong relationship ($r = +0.75$) between spring freshwater flow and upper Chesapeake Bay striped bass recruitment strength was reported for the years 1985-2007 (Chapter 3). The relationship between freshwater flow and recruitment strength was linked to a bottom-up control of recruitment in which climatology sets up hydrological conditions in the nursery habitat of striped bass and other anadromous fishes (Wood, 2000). Wet hydrological conditions during March through May promote higher prey abundances, enhance the spatio-temporal overlap between larval striped bass and zooplankton prey in the ETM and salt front (North and Houde, 2001, 2003, 2006), and result in higher feeding success and survival of larvae (Chapter 3). The findings in this chapter provide additional evidence for bottom-up control of recruitment, and support my hypothesis that larval growth is enhanced in high freshwater-flow years.

Larval growth was 58% higher in 2003 when the level of YOY juvenile recruitment was exceptionally high (11.9 per seine haul) compared to larval growth in

2001 when the level of juvenile recruitment was moderate (7.2 per seine haul). However, larvae in 2001 experienced warmer temperatures that were closer to the level (24 °C) associated with maximum growth (Rutherford and Houde, 1995; Houde, 1996). Annual differences in growth trajectories revealed that the rate of larval growth in 2003 exceeded rates in 2003 after the first-feeding stage (>10 dph). Findings in Chapter 3 showed that larvae fed more successfully in 2003 compared to 2001, and that annual differences in feeding success were most apparent for younger and smaller (<7.5 mm) larvae. Overall, faster larval growth in 2003 after the first-feeding stage, despite suboptimal temperatures for growth in this year, suggests that elevated prey levels and enhanced feeding conditions were responsible for faster growth in 2003. An important finding is that inter-annual variability in larval growth may be sufficient to generate observed differences in age-0 juvenile recruitment and year-class strength.

Fast larval growth has been linked to prey availability, larval survival and recruitment in other research on striped bass recruitment. The role of growth was evaluated in the Potomac River and upper Chesapeake Bay where the ratio of instantaneous growth to mortality (G/Z) was positively correlated with recruitment for three years in the Potomac and for two years in the upper Bay (Rutherford et al., 1997). In contrast, seasonal differences in larval growth and mortality during one year in the Hudson River indicated that survival of larval cohorts was not associated with fast growth (Limburg et al., 1999). However, the Hudson results indicated that larvae produced coincident with a spring bloom of cladoceran zooplankton experienced highest survival, suggesting a link between larval feeding success and survival.

Modeling research on striped bass recruitment in the Potomac River found no single factor that could explain the 145-fold variability in juvenile recruitment observed in that sub-population (Cowan et al., 1993). However, the model simulations did indicate that larval-stage growth and size-dependent mortality, both dependent on prey availability, could explain 10-fold variability in recruitment.

Growth: Inter-Annual Variability

Individual growth rates were highest on average in 2003 (Figure 4-7) when production of age-0 juveniles and recruitment strength were very high (Chapter 3). Average length-specific growth rate was 0.038 d^{-1} compared to an average rate of 0.024 d^{-1} in 2001. Mean larval size attained at 20 dph was 9.30 mm in 2003 compared to only 8.39 mm in 2001 (Figure 4-4). Growth rates that I estimated for striped bass larvae were similar to rates reported in two other studies of striped bass larval growth in Chesapeake Bay (Houde and Secor, 1996; Rutherford et al., 1997). Mean instantaneous daily growth of larval striped bass in the upper Bay in 1989 was 0.030 d^{-1} , (Rutherford et al., 1997), a rate in between my estimates for 2001 (0.024 d^{-1}) and 2003 (0.038 d^{-1}). My growth rates were also generally within the range of instantaneous growth rates ($0.025 - 0.048$) reported for the Nanticoke River in 1992-1993 (Houde and Secor, 1996).

Temperature may have contributed to inter-annual variability in larval growth. Temperature strongly affects growth of fish larvae (Houde in press) and larval striped bass is no exception (Rutherford and Houde, 1995). The temperature effects on

growth reported herein are consistent with results in other research. I detected a positive effect of temperature on larval growth up to 18 °C the highest temperature experienced by larvae in my study, and this finding is consistent with summarized results from other research on 41 larval cohorts of striped bass from Chesapeake Bay tributaries that reported a strong positive effect of temperature on growth up to 24 °C (Houde, 1996). Growth rates of striped bass larval cohorts for three years in the Potomac River and one year in the upper Bay ranged from 0.1 to 0.4 mm d⁻¹ (Rutherford and Houde, 1995). The authors reported a strong positive relationship between temperature and growth (0.02 mm d⁻¹ increase for each degree increase in temperature) (Rutherford and Houde, 1995) and proposed, based on their data, that temperature was the most important controller of striped bass larval growth rate in Chesapeake Bay. Growth rates determined by modal length progression of striped bass larval cohorts for two years in the Patuxent River ranged from 0.25 to 0.36 mm d⁻¹ (Campfield, 2005). Larval cohorts in the Patuxent River study grew faster earlier in the season in April and May when temperatures were lower, and the authors concluded that very warm temperatures (>25 °C) experienced by larvae in June were above the optimum for larval growth.

Other studies focused on larval striped bass growth found only minimal or no effect of temperature on growth rates. Growth rates of larval striped bass and white perch in the Hudson River ranged from 0.05 to 0.25 mm d⁻¹, rates lower than I observed in upper Chesapeake Bay. The Hudson River growth rates were at least weakly linked to temperature (Limburg et al., 1999), although prey level was believed to be more important. Temperature effects on growth were not detected in a study of

striped bass larvae during one year in the Patuxent River when mean growth rate was 0.17 mm d^{-1} and not related significantly to prey levels or temperatures (Secor and Houde, 1995).

Mean temperatures experienced by striped bass larvae in my study in 2003, when larval growth rate was high compared to 2001, were relatively low and below the temperatures associated with fastest reported growth. Larvae in my collections had experienced average temperatures $<17^{\circ}\text{C}$ throughout their life in 2003, while larvae in 2001 experienced average temperatures $\geq 18^{\circ}\text{C}$. In my research, larvae grew faster in 2003 at 16°C , the highest average temperatures experienced by larvae during that year, compared to larval growth at 16°C in 2001 (Figure 4-10). The faster growth rates observed in 2003 at low temperatures support the contention that feeding conditions were very favorable for larvae during this strong recruitment year, overriding the potential for temperature to be the major control over larval growth.

Growth-Dependent Larval Survival and Recruitment Variability

Findings reported here and in Chapter 3 strongly suggest that differences in growth between 2001 and 2003 resulted primarily from inter-annual variability in prey availability rather than effects of temperature or maternal investment. Larval feeding success was substantially higher in 2003 when prey concentrations and availability were high (Chapter 3). The percentage of feeding, early-stage larvae ($<7.5 \text{ mm}$) was much higher in 2003 (91%) than in 2001 (35%). The average growth trajectories of larvae in the two years indicated that length-at-age was similar until larvae reached 6.3

mm at >12 dph when effects of feeding success on larval growth can be detected. At that length, larval growth in 2003 surpassed lengths and growth rates of larvae in 2001 (Figure 4-7).

Average prey concentrations at the locations where striped bass larvae occurred in 2001 and 2003 were 2296 zooplankters m^{-3} and 15,877 zooplankters m^{-3} , respectively. Recruitment of age-0 striped bass in 2003 was higher (28.4 juveniles per seine haul) than all years on record for the MD DNR recruitment index since 1970, whereas recruitment in 2001 was near the long-term average (1957-present; 13.4 juveniles per seine haul). Prey concentrations in the upper Bay were twice as high in 1989 when recruitment was above average (19.4 juveniles per seine haul) than in 1988 when recruitment was low (7.3 juveniles per seine haul) (Rutherford, 1992). Larval growth in Rutherford's upper Bay study could only be determined in 1989 when sufficient numbers of larvae were collected. The 1989 growth coefficient (0.03 d^{-1}) fell between my results for 2001 (0.024 d^{-1}) and 2003 (0.038 d^{-1}) when recruitment strengths were average and strong, respectively. Further, in two years of very low age-0 recruitment, 1999 and 2002, prey levels were very low (mean < 2000 zooplankters m^{-3}) and were well below minimum levels required by striped bass larvae (Eldridge et al., 1981; Tsai, 1991).

Inter-annual differences in larval growth rates and weights at 20 dph were obtained by applying a length-weight relationship (Houde and Lubbers, 1986). Mean attained weights were 5.3 and 3.4 mg in 2003 and 2001, respectively. The instantaneous weight-specific growth rates (G) for larvae between 5 and 10 dph were similar in 2001 (0.20 d^{-1}) and 2003 (0.19 d^{-1}). However, G declined to 0.18 d^{-1}

between 10 and 15 dph in 2001 but increased dramatically to 0.27 d^{-1} in 2003. The high growth rates between 10 and 15 dph in 2003 were responsible for the 56% higher larval weights attained at 20 dph in 2003 compared to 2001.

Growth rate differences between 2001 and 2003, and their effects on stage-based mortality, are large enough in theory to explain the strong 2003 year class of striped bass. Significant correlations between the abundance of larvae and age-0 juvenile abundance strongly suggest that recruitment is fixed when larvae reach 10 mm in the Choptank River (Uphoff, 1989), and 8 mm in the upper Chesapeake Bay and Potomac River (Rutherford et al., 1997). If recruitment were fixed by 9.0 mm, a compromise between the Uphoff (1989) and Rutherford et al. (1997) threshold sizes, and if, for illustrative purposes, larval mean instantaneous mortality rates were equal in 2001 and 2003, the effect of stage-specific mortality on recruitment level can be estimated. The times to reach 9.0 mm were 19.2 days in 2003 and 23.0 days in 2001 based on the mean larval growth rates. A mortality rate of 0.2 d^{-1} for first-feeding (5.5 mm) larvae was applied based on a regression relating field-based mortality rates to larval length (Logan, 1985) that was similar to the value (0.18 d^{-1}) predicted from a regression relating larval size and mortality from pooled data for four striped bass year classes in Chesapeake Bay (Houde, 1997). Striped bass larvae exposed to that rate for an additional 3.8 days in 2001 would have suffered an additional 53% cumulative mortality before reaching 9.0 mm.

The 52 percent observed decrease in recruitment strength between 2003 and 2001 is similar to the additional cumulative mortality (53%) I estimated for 2001 larvae based on stage-based mortality alone. Abundance of a hypothetical cohort of 1

million striped bass larvae growing according to growth rates estimated for 2001 and 2003, and exposed to the average size-specific mortality rate of 0.2 d^{-1} , would be reduced to 21,494 and 10,052 individuals at 9.0 mm in 2003 and 2001, respectively. Similarly, striped bass larvae in the upper Bay in 1989 required 22.9 days to reach 9.0 mm if growing at the rate of 0.03 d^{-1} estimated by Rutherford et al. (1997). A 22.9 day stage-duration for 1989 larvae is similar to my estimate of 23.0 days required by larvae in 2001 to attain 9.0 mm and considerably longer than my estimate of 19.2 days in 2003. Recruitment in 1989 was moderate (19.4 juveniles per seine haul) and somewhat higher than recruitment in 2001 (13.4 juveniles per seine), but lower than recruitment in 2003 (28.4 juveniles per seine haul) when larval stage duration was shorter.

Mortality rates were unknown and could not be determined with the data available in 2001 and 2003. In the simple simulation analyses that I conducted, it was assumed that mortality rates were equal between years. This assumption is reasonable for the purpose of the exercise. However, results of the simulation could be misleading if larval mortality rates were higher in 2003. Higher mortality rates in 2003 seem unlikely given the faster growth rates in that year, and observed general negative relationship between striped bass larval growth and mortality rates. For example, one study reported a significant negative ($r=-0.67$, $p<0.001$) relationship between larval striped bass mortality rates and growth rates in laboratory experiments (Kellogg et al., 1996). Furthermore, larvae in 2001 that were growing slower would be smaller-at-age and possibly more vulnerable to predators (Miller et al., 1988; Bailey and Houde, 1989). The higher abundance of feeding-stage larvae, enhanced

feeding success, and higher growth rates in 2003 suggest that larval mortality rates were not higher, and may have been lower, in 2003 compared to 2001.

The benefits of faster larval-stage growth, as seen in striped bass in 2003, may include both shorter stage duration and a reduced effect of size-selective mortality. Logan (1985) summarized mortality rates (M) of striped bass larvae from several locations that indicated a decrease in M from 0.25 to 0.15 d^{-1} as larval size increased from 5-10 mm. Houde (1997) reported that mortality rate declined rapidly with respect to increasing weight in striped bass larvae as a power function, with power of -0.424. If mortality rate in the poor-growth year 2001 were higher than in the good-growth year 2003 because larvae were smaller-at-age in 2001, then stage-specific cumulative mortalities could differ even more under the combined effects of growth-rate and size-selective mortality.

Is There a Critical Stage for Larval Striped Bass?

The early-feeding stage of striped bass larvae may represent a critical stage in determining year-class strength. Results reported herein indicate a possible critical stage between 6.0 and 7.5 mm at which growth and mortality diverge markedly between years. In comparing larvae from 2001 and 2003, the divergence in length-at-age began at 6 mm. It seems probable that the relative recruitment level in 2003 may have been fixed at an earlier age than in 2001. Research evaluating effects of M , G , and M/G on survival and recruitment in five striped bass larval-stage cohorts (Houde, 1997) reported the highest recruitment potential for cohorts whose M/G ratio declined

to 1.0 at younger ages and at a smaller larval size, and that the most successful cohorts begin to accumulate biomass at small sizes (≤ 7.6 mm). Striped bass larvae in 2003, the strong recruitment year, were growing exponentially and larvae had substantially higher growth rates by 7.5 mm than in 2001, a year with lower recruitment. The accumulated evidence indicates that a combination of prey availability, associated feeding success, and hydrological variability (Chapter 3) are factors that control growth potential of striped bass larvae between first-feeding and 7.5 mm lengths. Variability in feeding success and growth rates provides a control over stage-specific mortality and recruitment potential.

Characteristics of Survivors

Characteristics of survivors may determine whether growth and larval size influence the probability of survival. There is a growing body of literature that demonstrates how larvae with specific size and growth-rate characteristics may be more or less likely to survive compared to individuals with average size and growth characteristics. While probability of death among individual larvae could represent a random process, this is unlikely in the sea. The usual expectation is that larger and faster-growing individuals will experience lower vulnerability to predation and higher survival probability (Anderson, 1988; Miller et al., 1988).

Most of the evidence for reduced striped bass larval mortalities at larger larval sizes is based on negative relationships between aggregate cohort mortality against the mean size of larvae in a cohort (Logan, 1985; Houde, 1997). One of my objectives

was to evaluate size-selective mortality directly using a longitudinal approach that back-calculated sizes of larvae at earlier ages. I hypothesized that surviving larvae would have grown faster and exhibited a larger size-at-age compared to average individuals sampled at earlier dates from the larval population. My results indicate that individual growth and size characteristics of striped bass larvae did influence their probability of surviving. Faster mean growth in 2003 was associated with higher survival.

Characteristics of surviving larvae relative to the average population were similar between years and supported the hypothesis that survivors exhibit higher growth and sizes-at-age compared to those characteristics in the average population of larvae. The faster growth and larger size-at-age of larval survivors compared to the average population of larvae in 2001 and 2003 indicate selection for fast-growing or larger individuals. In my study, no differences between survivors and average larvae were apparent until after age 10 dph in both years. Thus, differences in growth rate of early feeding-stage larvae, rather than size-at-hatching or yolk-derived nutrition, were responsible for selection of survivors. Larval survivors >13 dph in 2001 and 2003 were growing at high rates (2001, 0.30 mm d^{-1} ; 2003, 0.28 mm d^{-1}) compared to younger larvae. The high growth rates of survivors in 2003 were achieved despite cool temperatures (near 16°C) suggesting that prey was not limiting and that temperatures were adequate to support near-maximum growth.

Selection for fast growth in larval fishes has been reported frequently in the past decade and has been argued to be an important process supporting probability of recruitment success in individual larvae. For example, fast growth was selected for in

Atlantic cod larvae (Meekan and Fortier, 1996). Lengths of larval cod survivors diverged significantly from lengths in the average population at age 70 d, indicating that survivors benefited from a 13-d reduction in duration of the larval phase. In research on critical periods in larval rainbow smelt (*Osmerus mordax*) in the St. Lawrence River estuary and ETM, Sirois and Dodson (2000) found that survivors grew faster than larvae in the average population. Similarly, fast growing larval bluefish, *Pomatomus saltatrix* in the northwest Atlantic have a higher probability of survival (Hare and Cowen, 1997). More recent studies on coral reef fish recruitment revealed size-selective mortality in the damselfish *Neopomacentrus filamentosus* (Vigliola and Meekan, 2002) in which individuals that survived and settled on the reef were those that were larger at hatching and had grown faster during the planktonic stage.

Findings reported here provide evidence that fast growing striped bass larvae are positively selected for survival. However, the small sample sizes of survivor larvae adds uncertainty to the strength of this finding. There were only 6 and 10 larval survivors collected on the required dates in 2001 and 2003, respectively. Further, the short duration (2001=3 days, 2003=2 days) over which selection could occur during this study may have been insufficient to detect with certainty the final outcome of selection, or may not have been representative of selection processes operating over the complete 45-60 day spawning period of striped bass. Still, there is evidence of selection for survivors that is consistent with observations on many fishes. One earlier study focusing on striped bass larval growth and survival in the upper Bay and Potomac also found selection for fast growing larvae based on a positive relationship

between the age of larvae at capture and back-calculated lengths (Rutherford, 1992). The argument and support for selection of fast growing larvae needs to be confirmed and strengthened by conducting a selection analysis based on more larvae, and over a longer time period to confirm that selection for fast growth occurs in larval striped bass.

Previous research had recognized that striped bass recruitment in Chesapeake Bay is largely determined by survival variability during the larval stage. Other research (Uphoff, 1989; Rutherford et al., 1997) had concluded that striped bass YOY recruitment levels were fixed during the postlarval stage (8-10 mm). In some years, variability in year-class strength may result from spatial and temporal differences in larval prey availability, and effects on larval growth and survival, as reported here. Consequently, environmental factors that control prey availability, and its effects on feeding success and larval-stage growth, especially for first-feeding larvae, can play a major role in determining year-class strength of striped bass.

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Table 4-1. Summary of striped bass larvae collected in upper Chesapeake Bay for use in otolith microstructure analysis of age and growth during May for the years 2001, 2002, and 2003.

Year	Cruise Dates	Number of Larvae	Range of Standard Lengths (mm)
2001	May 7 - May 14	102	4.9 – 9.5
2002	May 6 - May 13	3	5.7 - 7.2
2003	May 13 - May 15	62	5.0 - 10.1

Table 4-2. Summary statistics for growth rates of two different age classes of striped bass larvae from upper Chesapeake Bay in May 2001, May 2002, and May 2003. Values are based on average growth rates of individuals calculated between time of capture and hatch date.

Year	Age	N	Mean	Median	Coefficient of Variation
2001	< 15 dph	64	0.25	0.26	0.21
	= 15 dph	38	0.23	0.22	0.16
2002	< 15 dph	3	0.27	0.24	0.22
	= 15 dph	NA	NA	NA	NA
2003	< 15 dph	39	0.24	0.24	0.18
	= 15 dph	22	0.27	0.28	0.16

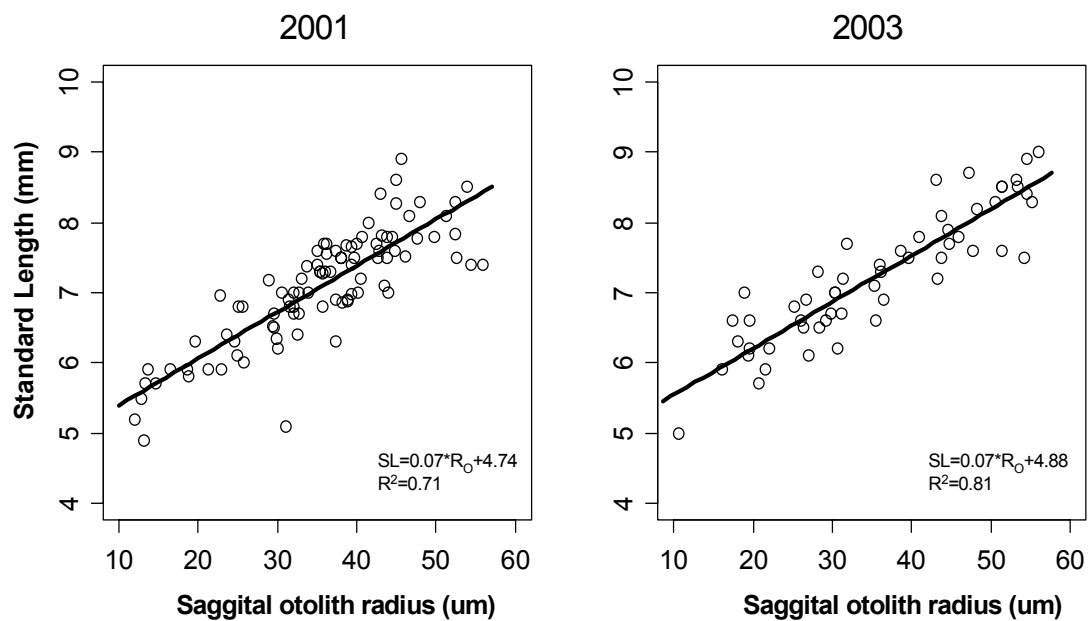


Figure 4-1. Relationship between striped bass larvae lengths and otolith radius for larvae collected in May 2001 and May 2003 in upper Chesapeake Bay.

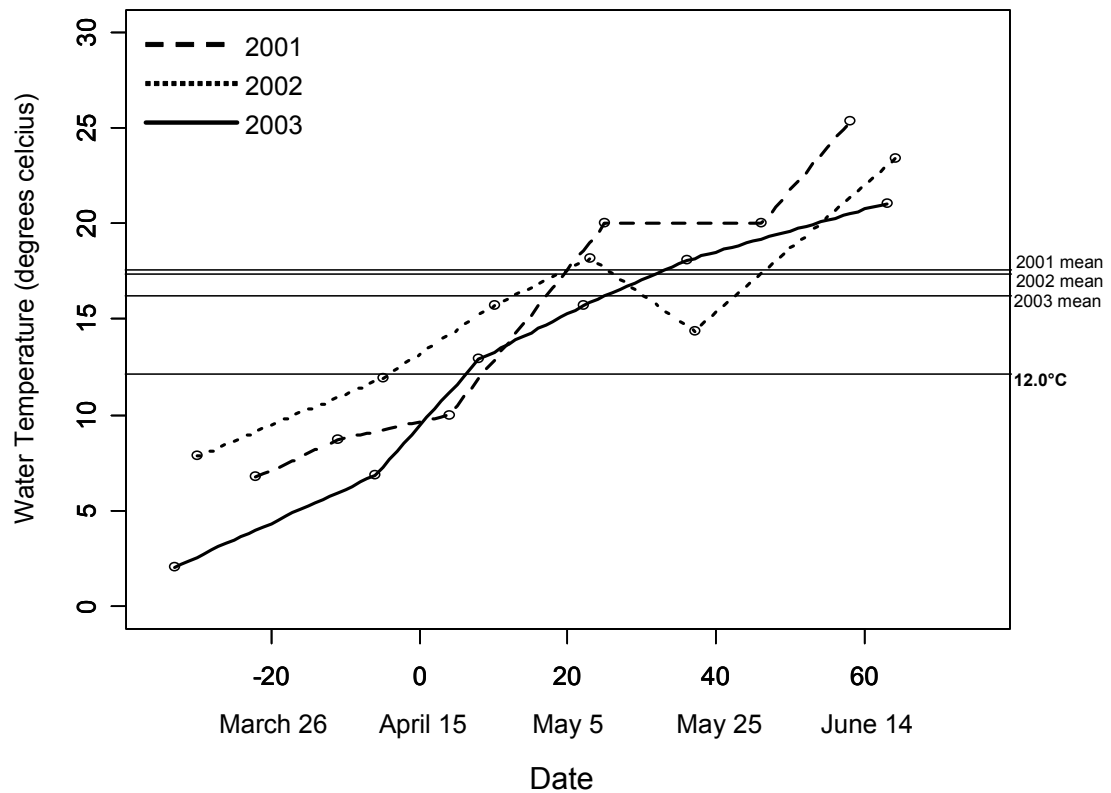


Figure 4-2. Temperatures in upper Chesapeake Bay during April and May in 2001, 2002, and 2003. Daily water temperatures are predicted from a regression based on BWI Airport daily air temperatures and biweekly temperatures measured at 1 m depth at a Chesapeake Bay Program monitoring station (CB2.1) in upper Chesapeake Bay. The horizontal lines at 12.0°C, 17.7°C, 17.7°C, and 16.2°C represents a low threshold temperature generally associated with the initiation of spawning, and the mean temperatures in 2001, 2002, and 2003 respectively.

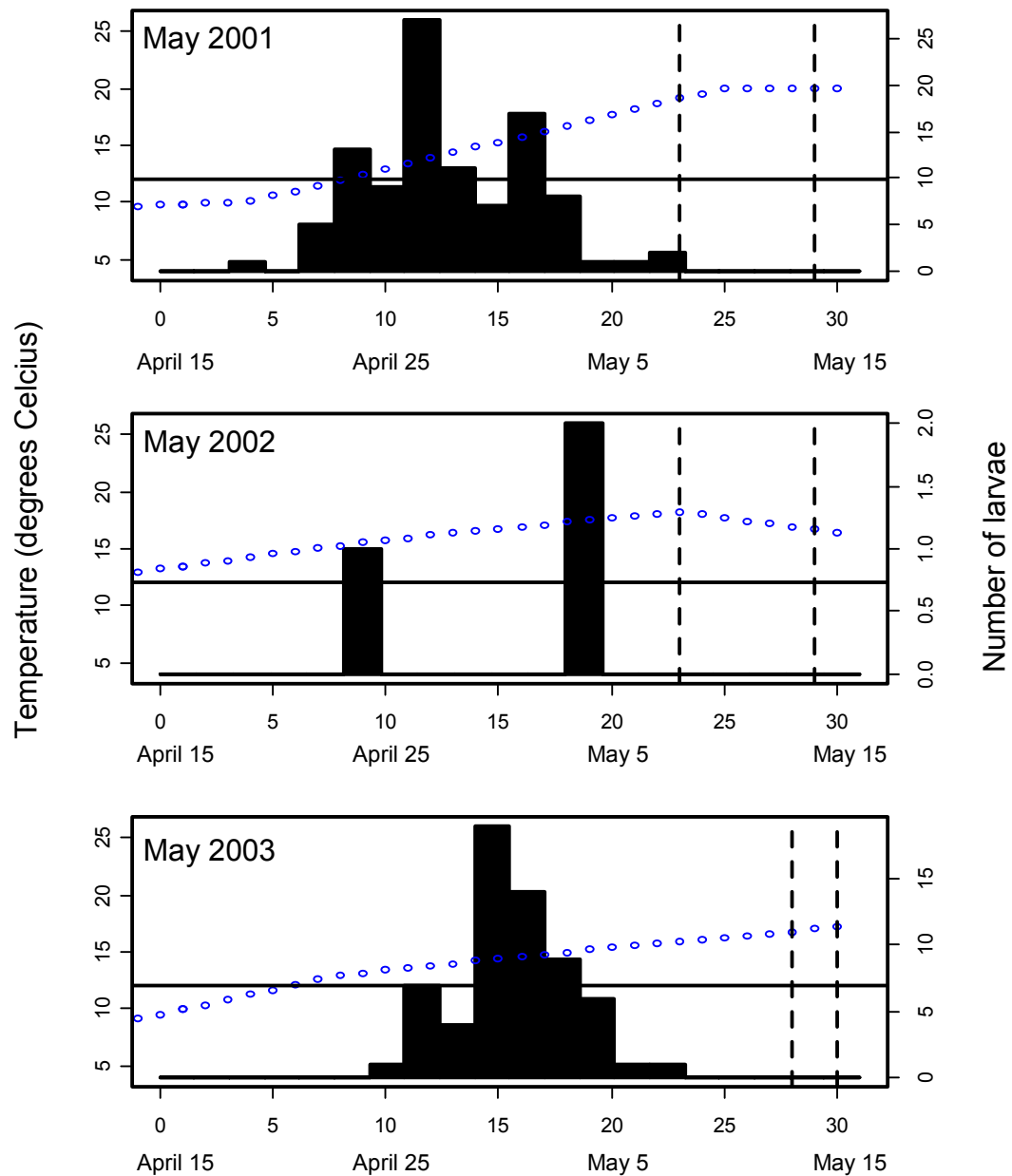


Figure 4-3. Hatch-date frequencies of striped bass larvae used in growth analyses and temperatures experienced by larvae (blue dotted lines) in the upper Chesapeake Bay during May 2001, May 2002 and May 2003. Cruise sampling dates are the intervals between the dashed vertical lines.

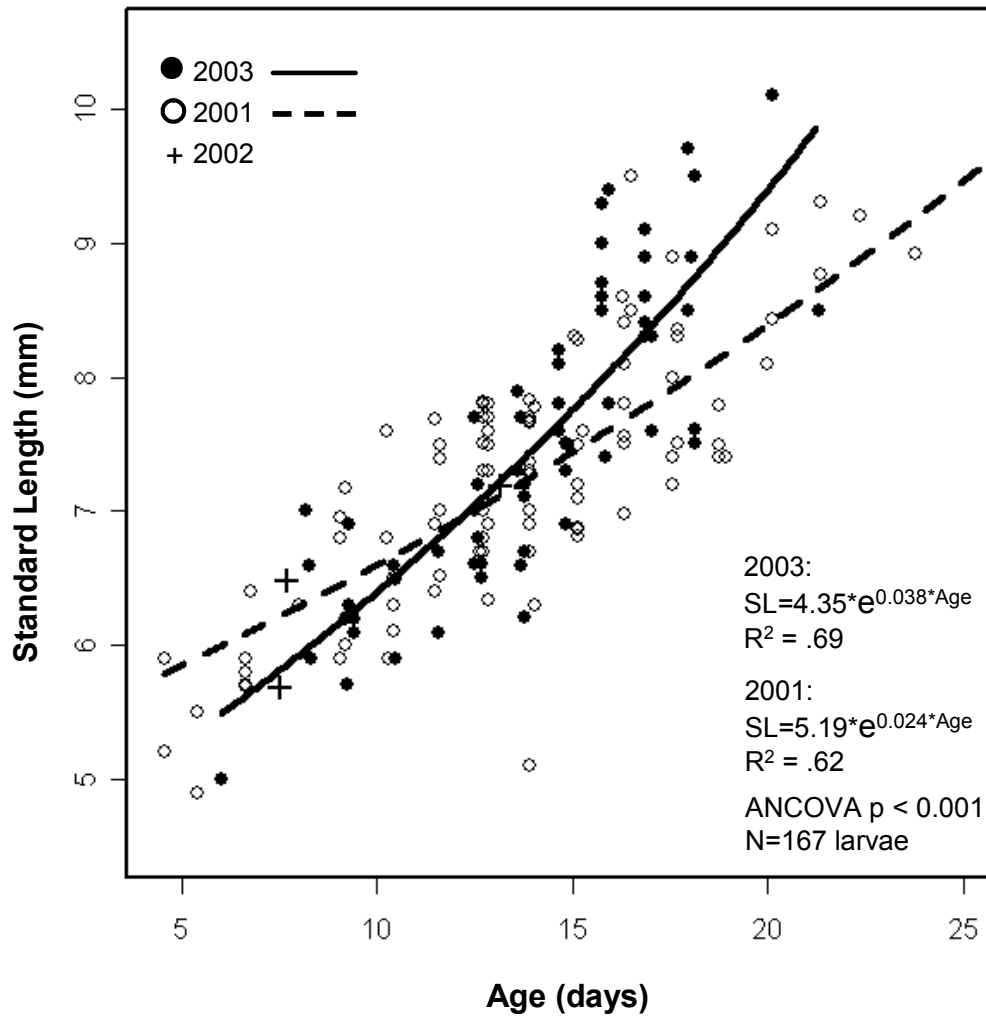


Figure 4-4. Mean growth rates of striped bass larvae in upper Chesapeake Bay during 2001, 2002, and 2003, based on exponential model fits of standard length on age (days post hatch) at the time of collection. Only three larvae are represented in 2002; no regression was fit.

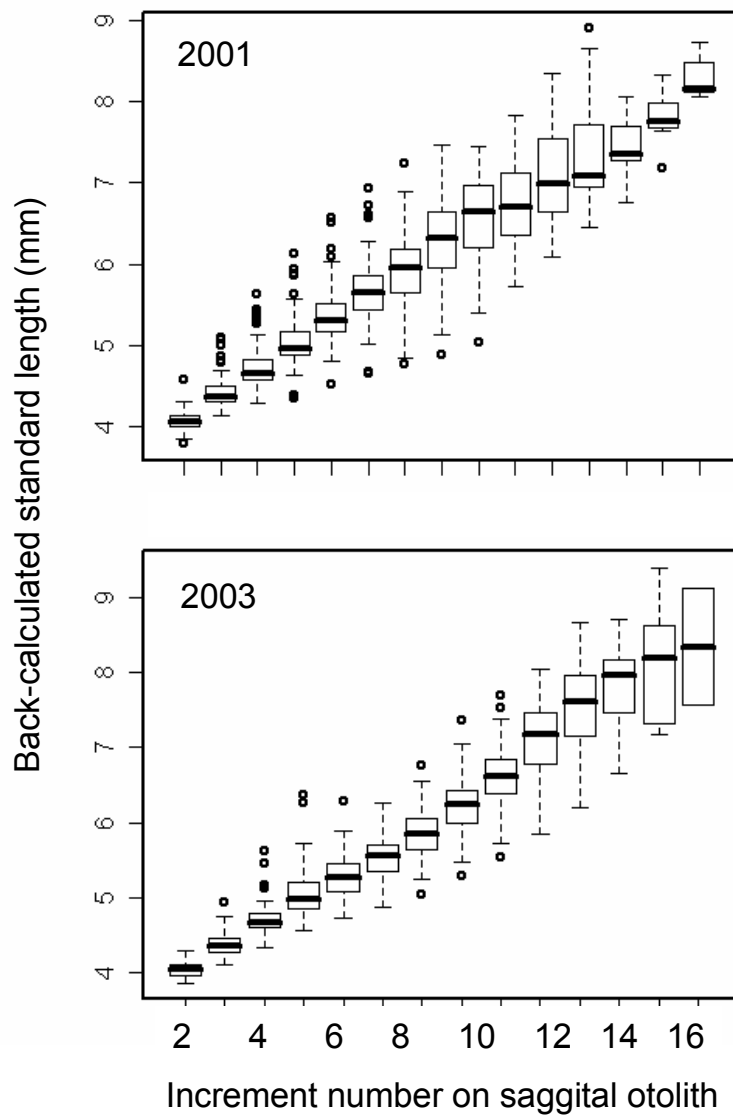


Figure 4-5. Boxplots showing distribution of back-calculated lengths at age for upper Chesapeake Bay striped bass larvae collected during May 2001 and May 2003. Solid black bar within the boxes represents the median larval length, the lower and upper boundaries of boxes represent the 25th and 75th percentiles of length, and the lower and upper whiskers represent the minimum and maximum lengths unless outliers are present. Open circles are outliers.

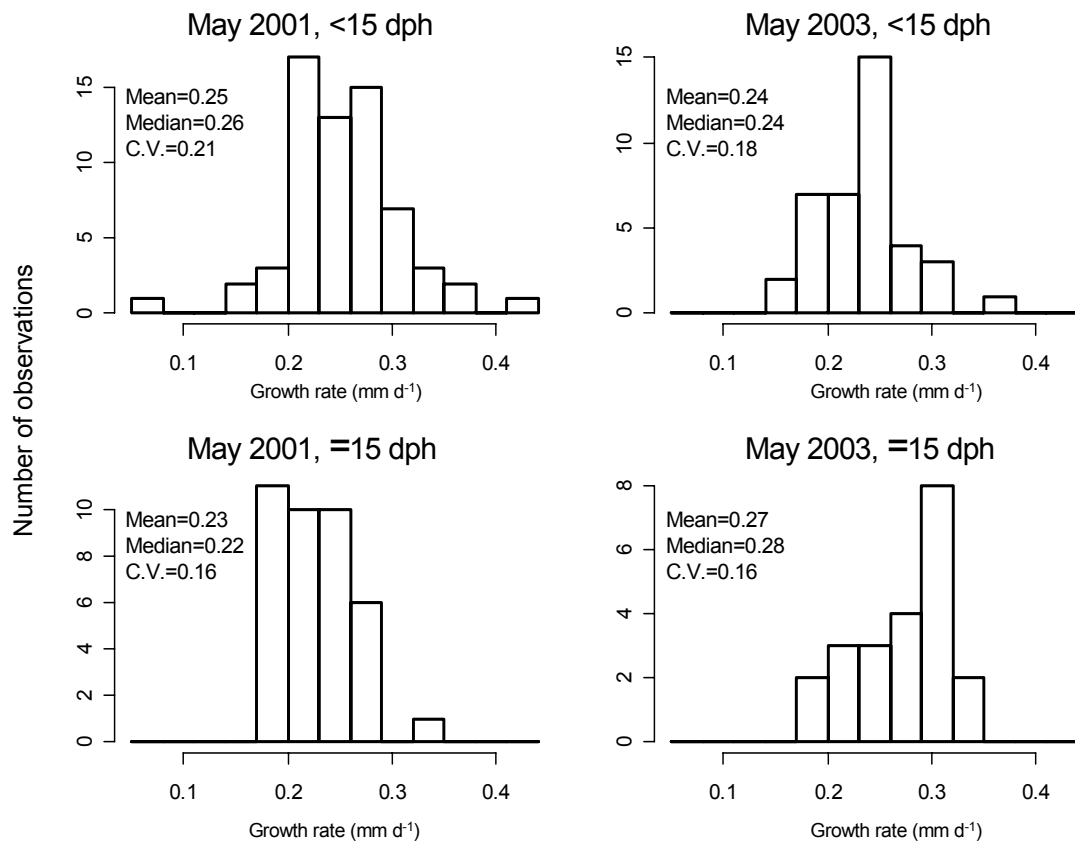


Figure 4-6. Distribution of individual growth rates (mm d⁻¹) of striped bass larvae < 15 days post hatch (dph) and ≥ 15 days post hatch in May 2001 and May 2003.

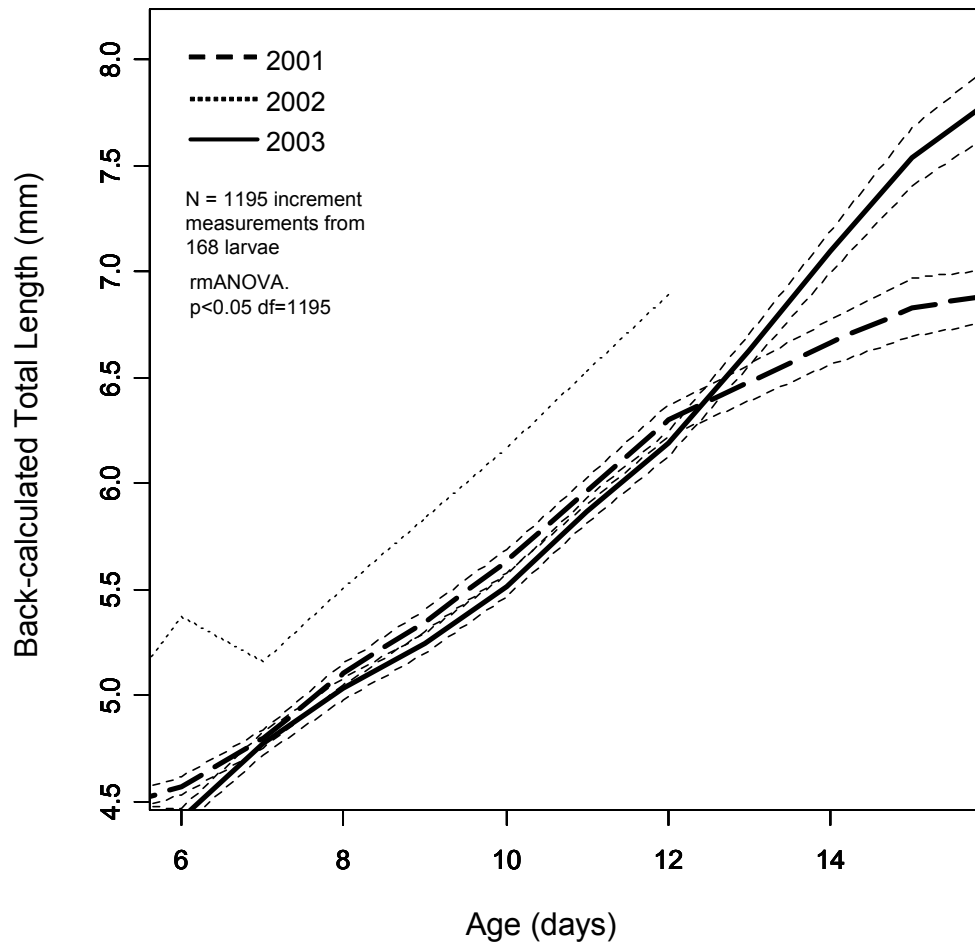


Figure 4-7. Growth trajectories for striped bass larvae constructed from mean back-calculated lengths of larvae collected in 2001, 2002, and 2003. The heavy lines represent the mean back-calculated lengths and the thin dashed lines represent 1 standard error. Data for 2002 included only three larvae, and no standard deviation was calculated.

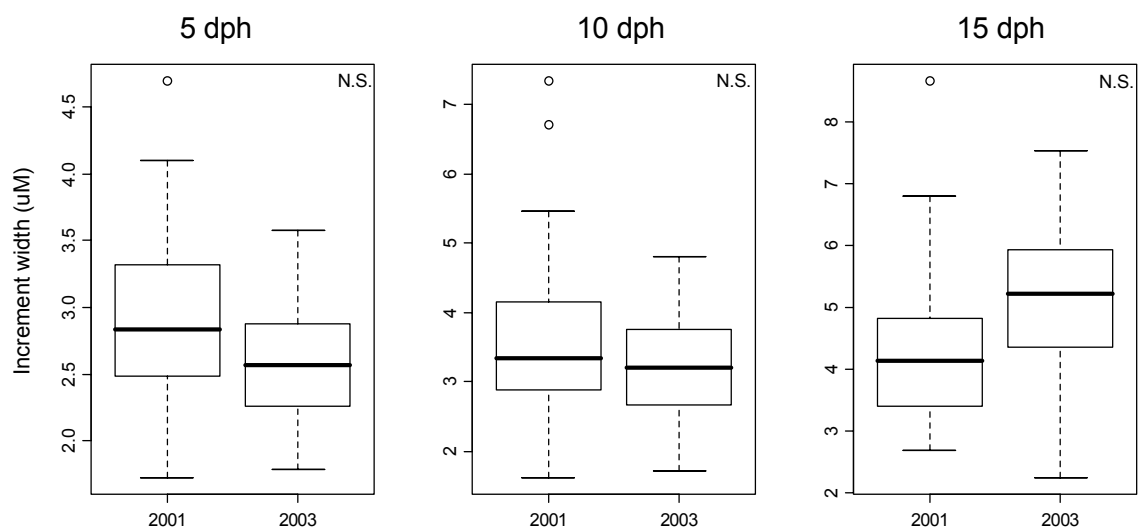


Figure 4-8. Boxplots of otolith increment widths of striped bass larvae at 5, 10, and 15 days post hatch (dph) in May 2001 and May 2003 in upper Chesapeake Bay. Solid black bar within the boxes represents the median increment width (μm), the lower and upper boundaries of boxes represent the 25th and 75th percentiles of increment width, and the lower and upper whiskers represent the minimum and maximum increment widths unless outliers are present. Open circles are outliers.

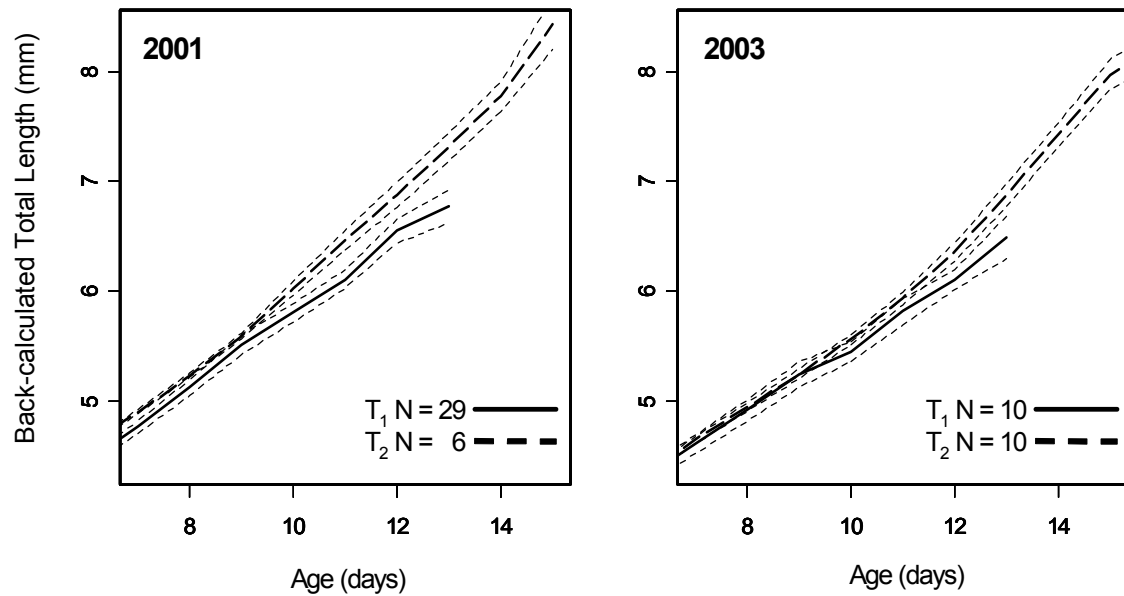


Figure 4-9. Characteristics of surviving larvae based on back-calculated lengths of striped bass larvae collected at two time periods during May 2001 and May 2003 in upper Chesapeake Bay. Larvae representing the average population (T1) were collected on May 8 in 2001 and May 13 in 2003, and the survivors (T2) were collected during May 11 through May 14 in 2001 and on May 15 in 2003. The bold lines represent the mean back-calculated lengths and the dashed lines represent the standard deviation.

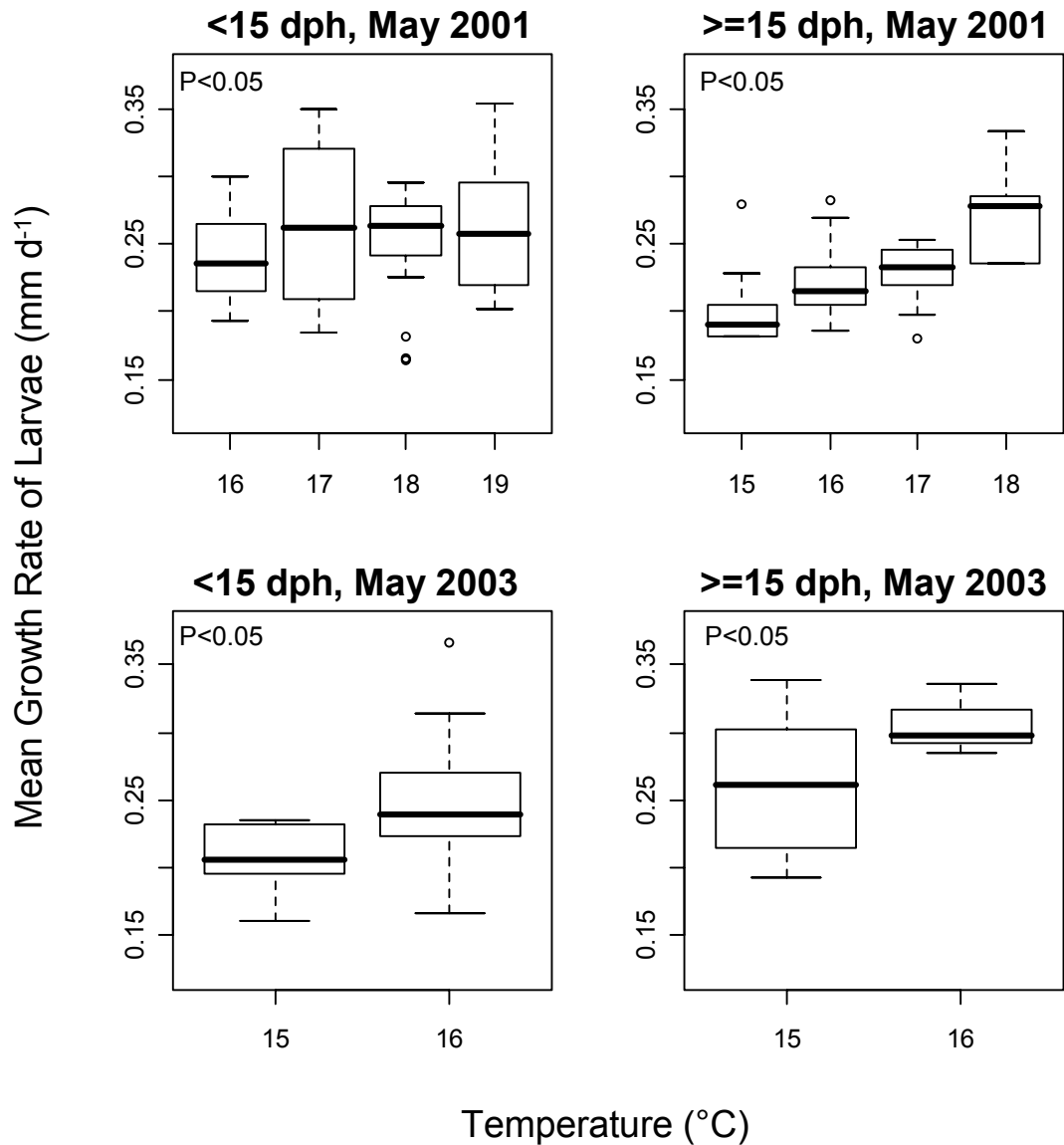


Figure 4-10. Effect of mean temperatures experienced by striped bass larvae between dates at hatch and collection dates with respect to growth rates of larvae <15 days post hatch (dph) and ≥ 15 days post hatch in May 2001 and May 2003. Solid black bar within the boxes represents the median growth rate, the lower and upper boundaries of boxes represent the 25th and 75th percentiles of growth rate, and the lower and upper whiskers represent the minimum and maximum growth rates unless outliers are present. Open circles are outliers.

CHAPTER FIVE

Density-Dependent Regulation of Recruitment in Chesapeake Bay Striped Bass

INTRODUCTION

Strong fluctuations in abundance of fishes usually are attributed to order-of-magnitude or greater variability in recruitments driven by variability in early-stage larval survival, the establishment of relative year-class strength early in life, and the persistence of dominant year classes through time (Hjort, 1914). Control over recruitment level will most likely operate on the abundant egg and larval stages (Cushing, 1975; Houde, 1989) where mortality and growth rates are highest and most variable, and the greatest changes in abundance are observed. Still, it is recognized that relatively small variability in dynamics during the long juvenile stage can have important consequences for regulation of recruitment in some populations (Sissenwine, 1984).

Despite high variability in year-class strength, variability in recruited abundances are lower than might be expected, given the high numbers of eggs and larvae, and the high variability in their mortality rates. This observation led some scientists to argue that strong density-dependent regulation must operate in most exploited populations that are resilient to heavy exploitation (Shepherd and Cushing, 1980). There are notable examples providing evidence for density-dependent regulation in fish populations. Extensive research on plaice *Pleuronectes platessa* L.

in the Southern Bight of the North Sea indicates coarse and fine controls over recruitment, where variability is generated and regulated, respectively (Van der Veer et al., 2000). Coarse controls over recruitment operate during the pelagic egg and larval stages of plaice (Brander and Houghton, 1982; Zijlstra and Witte, 1985; Van der Veer, 1986), while regulation occurs at the juvenile stage and acts to dampen variability generated in earlier life stages (Van der Veer, 1986). A meta-analysis on recruitments in 17 populations of marine demersal fish from the North Atlantic concluded that variability in year-class strength is generated at the larval stage, but regulation of year-class size occurs in the juvenile stage (Myers and Cadigan, 1993).

Despite many examples of density dependence, a controversy over regulation has persisted for several decades because evidence for compensation is usually minimal and ambiguous (Shepherd and Cushing, 1990) as is definition of the life stage(s) at which it operates (Myers and Cadigan 1993; Myers 2002). In a recent synthesis Rose et al. (2001) recommended a multifaceted approach to address the problem in which statistical evidence from long-term monitoring data is coupled with process-level understanding of the density-dependent mechanism.

Striped bass in Chesapeake Bay experiences large fluctuations in recruitment of young-of-the-year fish, partly in response to varying hydrological conditions (Ulanowicz and Polgar, 1980; Mihursky et al., 1981; Houde and Secor, 1996; Secor D.H., 1996; North and Houde, 2001, 2003; Martino and Houde, 2004) and San Francisco Bay (Turner and Chadwick, 1972; Kimmerer et al., 2001). For example, freshwater flow and its effects on biological processes operate to coarsely control egg and larval survival in Chesapeake Bay striped bass (North and Houde, 2001, 2003;

Martino and Houde, 2004). Freshwater flow during spring affects the spatial and temporal availability of prey for feeding-stage larvae (Chapter 3). Nonetheless, considerable fine-tuning of abundance can operate during the long juvenile stage, in which even small changes in mortality rate can have a major effect on age 3-4 recruited year-class strength.

Most research on recruitment variability of striped bass in Chesapeake Bay has been directed at egg and larvae survival. Recruitment level at age-0 (at approximately 100-150 days posthatch) in Chesapeake Bay striped bass was correlated with abundance of 10-mm larvae in the Choptank River from 1980-1985 (Uphoff, 1989), and recruitment was fixed by 8 mm SL in the upper Bay for 1988 and 1999 and Potomac River for 1987-1989 year classes (Rutherford et al., 1997). Similarly, during 1973-1977 abundances of post yolk-sac larvae from the upper Chesapeake Bay and Delaware River were correlated with the MD juvenile recruitment indices (Kernehan et al., 1981). My results (Chapter 2) show a significant positive relationship between age-0 recruitment and the abundance of feeding-stage larval moronids and alosines. Density dependence has not been detected or reported at the egg or larval stages of striped bass. A recent evaluation of density dependence in larval striped bass from the Potomac River was inconclusive (Rutherford et al., 2003).

Life histories of coastal-spawning and anadromous estuarine-dependent fishes rely on residency by early-life stages in estuarine nurseries. A specific hypothesis on density-dependent recruitment (“concentration hypothesis”) states that variability in recruitment is dampened for populations that concentrate during the juvenile stage compared to populations that do not concentrate at this stage. Recently, the hypothesis

was tested and shown to be supported for many populations (Illes and Beverton, 2000). Striped bass eggs and larvae are pelagic and occur in upper reaches of estuaries, usually within 10 km of the salt front (Rathjen and Miller 1957). Conspicuous centers of abundance occur near the salt front and ETM during high-abundance years (Chapters 2 and 3) when larval survival and juvenile abundance are high (North and Houde, 2003). The centers of concentrated larval abundance are maintained and still detectable 90 days later at the juvenile stage (Chapter 2) when these concentrated juveniles begin to consume benthic prey. Larval-stage striped bass feed pelagically on zooplankton until reaching a length of approximately 15 mm when, as juveniles, they begin to consume more benthic prey such as insect larvae, polychaetes, amphipods, and mysids (Boynton et al., 1981). The trophic transition from planktonic to benthic prey and a shift in location and concentration in demersal habitats may trigger density dependence in Chesapeake Bay striped bass, and could be one of the primary mechanisms regulating recruitment.

Density dependence has been detected and described in the juvenile stage of other populations of striped bass. For example, density-dependent mortality of juveniles was detected in the San Francisco Bay estuary (Kimmerer et al., 2000) and Hudson River (Hurst and Conover, 1998; Buckel et al., 1999). My preliminary dissertation results hinted at density dependence in juvenile striped bass in Chesapeake Bay (Martino and Houde, 2004). Common to all of these studies was evidence that regulation of recruitment commenced after the larval stage.

A primary goal of my research was to undertake a comprehensive evaluation of the recruitment process of striped bass in Chesapeake Bay. Chapters 2 through 4

are focused on larval-stage processes that generate variability in recruitments and which operate during spring months. This chapter emphasizes juvenile-stage processes that operate after the larval stage and continue through the first year of life. I hypothesized that density dependence operates at the juvenile stage and contributes importantly to regulation of year-class strength. Specifically, I address the following questions: 1) Does density-dependent growth occur in age-0 juvenile-stage striped bass in Chesapeake Bay? 2) Does density-dependent mortality operate at the juvenile stage? and 3) What are possible sources of density-dependent mortality?

MATERIALS AND METHODS

Juvenile Abundance and Sizes

The analyses are based on surveys conducted in major spawning locations in the Bay (Figure 5-1), including the mainstem upper Bay, the Potomac River, and Nanticoke River in Maryland, and the James, York, and Rappahanock Rivers in Virginia. These locations were chosen because together they represent a large proportion of the Chesapeake Bay striped bass metapopulation (Figure 5-1). In addition, data generally were more plentiful and available from these systems than from other nursery areas in the Bay. Juvenile striped bass abundances and lengths are from three data sources: Maryland Department of Natural Resources (MDDNR) recruitment seine survey (<http://www.dnr.state.md.us/fisheries/juvindex/index.html>), Virginia Institute of Marine Science (VIMS) recruitment seine survey

(<http://www.fisheries.vims.edu/trawlseine/sbhistory.htm>), and the NSF-funded BITMAX project (<http://www.bitmax.org/>). The two recruitment surveys provide annual juvenile abundance indices expressed as either arithmetic or geometric mean numbers of juveniles per seine haul. To adjust seining effort in the surveys for variable effort, I converted raw survey catches of striped bass juveniles to approximate densities on a per area basis (number m⁻²) by dividing raw counts by estimated area swept at each site. Area swept estimates for MD locations were based on distance the seine was pulled offshore and simple geometric relationship. The maximum area swept was ¼ the area of a circle when the seine could be fully extended from shore. Less than optimal deployments approximated the area of a partial trapezoid.

$$\text{Maximum Area Swept} = 1/4\pi \cdot D^2 = 729 \text{ m}^2$$

$$\text{Reduced Area Swept} = D^2 \cdot (\sqrt{L_s^2 - D^2}) + (0.5 \cdot (D \cdot (L_s - \sqrt{L_s^2 - D^2})))$$

Where D = distance offshore, and L_s=length of the seine (30.5 m).

Distance offshore was not recorded during early years of the VIMS seine surveys, an additional source of variability in the data. Consequently, the VA data were used only in selected analyses requiring less rigorous standardization. For the VIMS data, I calculated an average area swept (285 m²) based on the the average measurement for distance offshore recorded in the most recent years (2001-2003).

My research was a component in an interdisciplinary project (NSF-BITMAX) whose goal was to evaluate the role of the estuarine turbidity maximum (ETM) in

Chesapeake Bay on mesozooplankton and fish population dynamics and production. Three BITMAX research cruises were conducted in the upper Chesapeake Bay each year during May, July, and October in 2001, 2002, and 2003. The May cruises surveyed zooplankton and ichthyoplankton above, within, and below the ETM. Age-0 juvenile striped bass that are analyzed in this chapter were collected during the July and October BITMAX cruises.

BITMAX cruises commenced with a CTD survey along the axis of the upper Bay, starting at the Bay Bridge near Annapolis, MD and progressing to the head of the Bay near Turkey Point (Figure 5-1; see Figure 2-1 in Chapter 2 for a more detailed illustration of the upper Bay study location). The hydrographic profiles from the CTD casts were used to locate and describe the ETM region. The sampling domain was an approximately 50-km track along the axis of the upper Bay and encompassed sites above, within, and below the ETM.

Juvenile striped bass and other fishes were sampled with an 18 m² mouth-opening midwater trawl, with a 6-mm codend liner. The trawl was towed for 20 min in 2-min stepped oblique segments from surface to bottom. Striped bass and other fishes were counted, measured, and their aggregate biomasses determined at each station. A CTD cast preceded each midwater-trawl tow.

Environmental Data

Data from the Chesapeake Bay Program's Water Quality Monitoring Surveys (CB-Program, 2006b) were compiled for the upper Bay to provide mean

temperatures, salinity, and dissolved oxygen during the summer growth season. The NOAA Thomas Point Buoy daily water temperature data provided winter water temperatures that are not always available from the Chesapeake Bay Program.

Estimating Growth Rates

Growth-in-length was estimated using three methods and three data sources to provide at least one estimate of growth rate for each of six different sub-populations for periods covering at least ten years (Table 5-1). The first estimate of juvenile growth was based on the length attained at the end of the first growing season. These retrospective analyses were conducted from 1980-2003 for locations having the most complete data for the longest period with consistent sampling. Juvenile lengths and abundances are from the Maryland Department of Natural Resources (MDDNR) Juvenile Recruitment Survey and from the William and Mary, Virginia Institute of Marine Science (VIMS) striped bass seine surveys.

Juvenile growth also was estimated from mean and median lengths of surveyed striped bass during and at the end of the growing season, with initial dates in July for all surveys and terminal dates in September for MDDNR and VIMS surveys, and October for BITMAX surveys. Individual fish in the MDDNR surveys were aged by MDDNR by examination of monthly length-frequency distributions and scales to separate age-0 and age-1 striped bass. Fish in the VIMS surveys were separated into age-0 and age-1+ groups by VIMS based on inspection of modes in bi-weekly length-frequency distributions by VIMS.

Growth rates of YOY striped bass, based on MDDNR seine-survey data, were estimated from the difference in median lengths between July and September for 1991-2003 in the Potomac River and 1980-2003 in the upper Bay. This analysis was restricted to the upper Bay and Potomac River, which contain the two largest striped bass subpopulations. Striped bass in the length-frequency analysis were assigned to 3-mm bins to provide sufficient sample sizes and resolution of size structure for the growth rate analysis.

Estimates of juvenile striped bass growth in the upper Bay during 2001-2003 also were obtained from fish sampled in BITMAX midwater-trawl collections, based on modal progression of lengths. This analysis included collections made at relatively high spatial and temporal resolution throughout the upper Bay during July and October. This sampling design allowed growth rates to be estimated from modal-length progression that could be compared with growth estimates from the MDDNR seine-survey monitoring.

To estimate growth rates, normal distributions were fit to monthly length frequencies from the BITMAX surveys in 2001, 2002, and 2003. The Mclust (Fraley and Raftery, 2002) function in the “R” statistical package was used to identify length modes in monthly data. The Mclust routine in “R” is based on the expectation-maximization (EM) algorithm (Dempster et al. 1977; McLachlan and Krishnam 1997) that separates individual normal distributions. Both unimodal and multimodal monthly length distributions were common in YOY striped bass from the upper Bay. I limited the number of monthly modes to three after examining histograms of monthly length frequencies, and one or two modes usually provided acceptable fits to

the observed length data. Annual growth rates for the upper Bay were estimated according to the following equation.

$$G_{SubPopulation} = \frac{\sum_i^n p_i ML_{Fall} - \sum_i^n p_i ML_{August}}{t}$$

G=Growth Rate; ML=Modal Length; p=Proportion in mode *i*; t= 30 days
between surveys

Automated scripts were written in R (R Development Core, 2005) to facilitate rapid objective estimation of growth. This growth analysis procedure was compared with the other growth estimation approaches, based on length attained and differences in median lengths between time periods.

Biotic and abiotic variables were analyzed to determine possible relationships to growth of YOY striped bass. General linear model regression was used to determine which variables were predictive for growth in the upper Bay and Potomac River for years in the surveys.

Density-dependent Growth

I tested for a significant negative relationship between length attained and age-0 juvenile abundance for six subpopulations of striped bass to determine if growth was density dependent. This relationship was evaluated by applying general linear models and negative power models. The linear model describes a relationship where the rate

of decline in length is constant across all abundance levels. A negative power relationship indicates a steeper decline in length attained at relatively low but increasing abundance levels, but more moderate declines at higher abundance levels. The negative power function may be indicative of effects of prey-limited growth because per capita prey resources should decline according to $1/\text{juvenile abundance}$ (Grant and Imre, 2005). I also evaluated possible density-dependent growth in the upper Bay and Potomac River with general linear models, testing for significant negative relationships between abundance and estimated growth rates.

Benthic Prey Resources

To evaluate possible effects of benthic prey availability on age-0 striped bass growth, juvenile lengths and benthos monitoring data were analyzed in the upper Bay and Potomac River. Benthic organism abundance data from the Chesapeake Bay Program (BayProgram, 2006) were analyzed to estimate total and per capita prey availability among years and nursery locations. This analysis was conducted for years 1989-2003 in the upper Bay and 1991-2003 in the Potomac River. Analyses were restricted to the upper Bay and Potomac River because of data availability and quality.

The benthic invertebrate monitoring surveys (CB-Program, 2006a) consist of three samples at fixed stations and one sample at several random stations throughout the mainstem Bay and tributaries. Organisms are collected in box corers and grabs. Samples are sieved (0.5 mm screen) and organisms and detritus remaining on the screen are preserved. I calculated mean annual indices of benthic prey availability for

age-0 juvenile striped bass based on benthos samples collected in September each year. I used all samples from the tidal freshwater, oligohaline, and mesohaline segments of this survey, which typically resulted in 25-30 samples per year (CB-Program, 2006a). Taxa were excluded from analysis if less than 500 individuals were collected over the entire duration of the benthos survey. More than 100 benthic invertebrate species were included in the initial analysis. They were aggregated into five broad taxonomic groups including amphipods, polychaetes, decapod and mysid shrimp, clams, and chironomids.

Benthic prey density constitutes a coarse index of prey available to age-0 striped bass for comparison among locations and among years within locations. At each location, a “total benthic prey index” was the total number of individuals per square meter. The conversion of raw counts to mean number of individuals per square meter was undertaken by applying gear conversion factors (CB-Program, 2006a). The index consisted of all amphipods, polychaetes, and shrimp, which are known to be dominant prey of age-0 striped bass. The data used in this study included 29 polychaete, amphipod, and decapod shrimp species or taxonomic groups. Samples were dominated (47 %) by two species, including the amphipod *Leptocheirus plumulosus* (maximum size = 4 mm) and the polychaete *Streblospio benedicti* (maximum size = 6 mm). Clams were excluded because they are important prey of age-0 striped bass only during late fall and winter (Hartman and Brandt, 1995). Chironomids were excluded because they were not important prey of juvenile striped bass in Chesapeake Bay (Hartman and Brandt, 1995).

The relationship between benthic prey resources and age-0 striped bass growth, expressed as mean length attained in September, was evaluated by fitting the Holling Type II, a modified Michaelis-Mentin, equation (Holling, 1959).

$$Length = \frac{L_{max} [Resource]}{K_M + [Resource]}$$

L_{max} is the maximum length attained in September at saturation prey densities, K_m is the half-saturation constant, i.e., prey density where length attained is one half the maximum, and 'Resource' is the total benthic prey index. The model describes the asymptotic increase in length attained with respect to prey level. The Holling Type II model was chosen because growth was assumed to be limited by per capita prey availability. Under that assumption, consumption and maximum growth would occur at intermediate prey densities. Prey samples were collected during September, 1-2 months after striped bass juveniles begin to consume benthic prey. Thus, the approach allows evaluation of benthic prey as a determinant of age-0 juvenile growth during summer. The approach did not allow determination of whether observed benthic prey abundance was due to annual differences in benthic prey production and abundance or due to annual differences in prey consumption by juvenile striped bass.

Juvenile Striped Bass Diets

Gut-content analysis of age-0 striped bass from BITMAX trawl samples for years 2001-2003 was conducted to evaluate diet composition and feeding success, and to

compare inter-annual variability with growth rates. This analysis of feeding success and diet composition was undertaken to determine if prey-limited growth might be a mechanism to explain density-dependent juvenile growth. Ethanol-preserved, age-0 striped bass were weighed to the nearest 0.1 g. Stomachs were removed and weighed, and gut contents were sorted and identified under a dissecting microscope. Individual prey lengths were measured with an ocular micrometer; prey items were aggregated by taxonomic group and weighed.

Consumption demand, growth potential, and bioenergetics modeling

Monthly consumption demand by age-0 striped bass was estimated to evaluate monthly and inter-annual differences in population consumption demand among years. Maximum consumption potential (C_{\max}) was estimated for upper Bay age-0 juveniles during July, August, and September for the years 1989 through 2003. Weight-specific maximum consumption was based on experimentally-determined parameter values and the reported function relating age-0 striped bass consumption to weight (Hartman and Brandt, 1993):

$$C_{\max} = 0.302W^{0.252}$$

where W is wet weight (g). This equation for maximum weight-specific consumption was modified to account for effects of temperature on biological rates (Thornton and Lessem, 1978). Temperature-adjusted consumption is:

$$C_{\max} = 0.302W^{0.252} f(T)$$

For age-0 striped bass, 98% of weight-specific C_{\max} is realized at temperatures between 21.6 and 22.7 ° C; temperatures above and below this range reduce C_{\max} in a dome-shaped response (Hartman, 1993). For my analysis, monthly mean temperatures were based on Chesapeake Bay Program monitoring at upper Bay station CB2.1 which in most years is 5 to 10 km above the limit of saltwater intrusion (CB-Program, 2006b). Temperatures from July, August, and September of each year were used for this analysis. Mean weights of age-0 striped bass were estimated from mean lengths in MDDNR surveys using a total length-weight relationship that I derived from lengths (TL) and wet weights (W) of juveniles from BITMAX cruises in 2001-2003:

$$W=5E-06TL^{3.13}$$

Consumption demand estimates for individual fish were scaled up to population consumption demand on a per area basis using monthly age-0 striped bass density (no. m⁻²) estimates for years 1989-2003.

The Wisconsin bioenergetics model (version 3.0) (Hewett, 1992) was used to evaluate effects of annual differences in mean temperatures and temperature trends on growth potential and the proportion of consumption demand realized by age-0 striped bass in the upper Bay from 1989-2003. The bioenergetics modeling was applied only to the upper Bay sub-population which was sampled well by MDDNR surveys and the BITMAX program. The bioenergetics simulations were run using the striped bass juvenile parameterization provided in Hartman (Hartman and Brandt, 1993). All simulations were run from calendar day 195 through 255 to match sampling dates when length data were available. Daily water temperatures (°C) were predicted from daily air temperatures at Baltimore-Washington International Airport (BWI) airport. I

derived a relationship between bi-weekly measured water temperatures at monitoring station CB2.1 in the upper Bay (CB-Program, 2006b) and BWI air temperature from 1989-2003:

$$\text{Temperature}_{\text{water}} = 0.8427 * \text{Temperature}_{\text{Air}} + 5.0545$$

$$r^2 = 0.8541$$

Bioenergetics simulations were run using initial and final weights of age-0 striped bass, predicted daily water temperatures, and percent diet composition from a previous study (Hartman and Brandt, 1995) as inputs to the model. Diet composition for each year was not available and I assumed the effect of differences in inter-annual consumption of prey types would be minimal compared to total biomass of prey consumed. The model calculated the p-value, the proportion of C_{max} realized, an indicator of prey availability. The p-value is closer to 1 when prey availability is not limiting. Two simulations were run for each of the 15 years, 1989 through 2003, for a total of 30 simulations. One simulation was run for the period July to August and another for the period August to September. For each simulation, initial and final striped bass weights were based on mean lengths in July, August, or September from the MDDNR seine survey converted to weights using my length-weight relationship. The bioenergetics model was fit to the final weight in each simulation and provided an estimate of the p-value for each year.

Age-0 Mortality Rates

Mortality of striped bass over the first year of life was estimated from survey data on abundances from the upper Bay and Potomac River subpopulations (Table 5-2). The decline in mean numbers of age-0 juvenile (no m⁻² swept by seine) from July-August of year t to July-August of year $t+1$ was used to estimate instantaneous daily mortality for each annual cohort. Mortality rates were calculated for each year t as:

$$M = \frac{\log_e (Abundance)_t - \log_e (Abundance)_{t+1}}{365d}$$

where $Abundance_t$ and $Abundance_{t+1}$ equals the mean number of juveniles m⁻² during their first (age-0) and second summers (age-1). This analysis was conducted on striped bass from the upper Bay and Potomac River, but not on the less consistently sampled other systems.

Juvenile Density-dependence

Two tests to evaluate density-dependent mortality in young-of-the-year striped bass were conducted. The first method tested for a significant positive relationship between estimated mortality rate and abundance using traditional linear regression. The second method was the log-log unit slope test. The log-log unit slope tests the relationship between $\log(abundance)_t$ and $\log(abundance)_{t+1}$, where the null hypothesis is the slope=1. A slope coefficient significantly <1 indicates density-dependent survival (Myers and Cadigan, 1993). In the presence of error in measurements of abundance this test can suffer from inflated type I error unless the magnitude of

measurement error is known *a priori* (Myers and Cadigan, 1993). Another potential concern is density-dependent catchability, e.g., from density-dependent movements among habitats. This concern was evaluated by comparing data from multiple surveys of striped bass juveniles conducted in different habitats and locations in the Bay and tributaries. I compared catches of juveniles in primary nursery habitat with adjacent (downbay) habitats to determine if density-dependent migration losses of juveniles might be problematic in high-abundance years.

Mortality and Environmental Factors

Stepwise, multiple linear regressions were run to determine what factors best explained mortality-rate variability in age-0 striped bass among years in the upper Bay and Potomac River. Variables determined to be non-normally distributed were log-transformed before inclusion in this analysis. The factors considered for inclusion in the multiple-regression analysis on mortality included mean summer salinity, mean summer temperature, age-0 juvenile abundance, mean length of age-0 juveniles in September, mean winter temperature, mean winter salinity, and the interaction between mean length of YOY striped bass and winter temperature.

Recruited Year-class Strength

A statistical model was developed to forecast recruited year class strength of striped bass in the upper Bay and Potomac River. The model included factors judged most important for survival of both larval and juvenile-stage striped bass. This model

then was used to predict recruited abundance (size-selectivity-corrected catch-per-unit-effort) of age 3-5 striped bass on the spawning grounds as determined in gillnet surveys conducted each spring by MDDNR. Two variables, age-0 juvenile abundance and mean winter temperature, were selected for inclusion in a model to forecast age-3 through age-5 striped bass abundance. Individuals 3 to 5 years old appeared to be fully recruited to the gillnet monitoring survey but had been exposed to fishing mortality for ≤ 3 years. Abundance data from gillnet surveys were available for years 1985-2002. My analysis and model focus on the 1989-2003 year classes; adult abundance data at age-5 were only available for the 1989-1997 year classes.

RESULTS

The mean densities of YOY striped bass in upper Chesapeake Bay from 1989-2003 ranged from 0.003 to 0.081 m^{-2} , with highest values in 1992 and 2003, respectively. Maximum densities at individual sampling sites ranged from 0.025 to 0.471 m^{-2} with lowest and highest values in 2002 and 2003, respectively (Table 5-3). Mean lengths from September seine surveys varied moderately (coefficient of variation C.V. = 11 %) and ranged from 67.8 mm in 1994 when mean juvenile density was 0.036 m^{-2} to 104.5 mm in 1992 when mean density was 0.003 m^{-2} (Table 5-3). The maximum juvenile density was 0.471 m^{-2} in 2003 when juveniles attained mean length 79.6 mm.

Lengths attained by YOY striped bass in the upper Bay from 2001-2003, based on BITMAX, October midwater-trawl surveys conducted in deeper channel habitats

were smallest in the year of highest juvenile abundance (2003) and biggest in the lowest juvenile abundance year (2002) (Figure 5-2, $p < 0.01$).

Based on the seine-survey data, the pattern of small lengths in high-abundance years and larger lengths attained in low-abundance years was consistent across all sub-populations, with the exception of the Potomac River (Figures 5-3 and 5-4). A negative power model relating lengths to abundances provided a better fit to these data than a general linear model in five of the six locations (Table 5-4). The negative effect on growth was most pronounced as abundance increased from low to moderate levels, compared to diminishing rate of declines in growth at moderate to high abundance levels, which is consistent with a negative power model for density-dependent growth.

Growth rates, estimated from the difference in median lengths between August and September, also declined significantly ($p < 0.05$) as juvenile striped bass abundance increased in the upper Bay (Figure 5-5). There was no significant relationship between growth rates and mean lengths in July, the earliest sampling month when the youngest juveniles recruit to the survey gear. The lack of a relationship for July suggests that differences in juvenile size and growth-rate had not yet developed sufficiently to be revealed or that these relationships were related to processes occurring later in the summer. In the Potomac River, juvenile sizes during summer were not related to abundance. Growth rates of YOY striped bass in the Potomac were unrelated to either abundance or July lengths (Figure 5-6).

Analysis of modal length progression on BITMAX midwater-trawl data provided additional growth estimates, based on samples collected from the upper Bay during 2001-2003. Results were similar to growth estimates based on seine- survey

data (Figures 5-5 and 5-7). The two methods to estimate growth rate produced similar results. In the median-lengths method, fastest growth occurred in 2002, a low-abundance year, at 1.4 mm d^{-1} and slowest growth occurred in 2003, a high-abundance year, at 0.4 mm d^{-1} . In the modal lengths progression method, fastest growth rate, 1.3 mm d^{-1} , occurred in 2002 and slowest growth, 0.25 mm d^{-1} , occurred in 2003 (Figure 5-5 and Figure 5-7).

Consumption Demand, Prey Supply, and Bioenergetics Modeling

Age-0 striped bass diets in the upper Bay were primarily dominated by benthic prey including mysids, polychaetes, and amphipods. The diet analysis revealed higher feeding success in low- compared to high-juvenile abundance years based on median number of prey in guts (Figure 5-8). The diminished stomach contents in high-abundance years is consistent with a decline in per capita prey availability (Figure 5-8).

Population-level consumption demand ($\text{g m}^{-2} \text{ d}^{-1}$) of upper Bay juveniles generally increased through summer for all years from 1989-2003 as temperature and individual striped bass weights increased, although consumption demand peaked in August in some years and September in others. For these years, the rank order of juvenile abundances remained largely unchanged from July through September (Figure 5-9). Annual rank orders of mean juvenile weights and population consumption demand often shifted between months when weights and consumption were compared (Figure 5-9). In general, mean weights in low-abundance years were

>4 g by September, regardless of initial weights in July while mean weights during high-abundance years usually were ≤ 4 g, especially if initial weights in July were <2 g. However, despite higher mean lengths and weights in low-abundance years, population-level consumption demand was consistently lower when compared to high-abundance years (Figure 5-9).

Bioenergetics modeling of YOY striped bass growth and consumption in the upper Bay indicated that consumption demand of juveniles (C_{\max}) is not met during years when juvenile abundance is moderate to high (Figure 5-10). Simulations were run to determine the proportion of C_{\max} realized for the period between July and August, August and September, and July through September for each of the years 1989 through 2003. The proportion of C_{\max} realized (p-value) indicated that maximum consumption was only attained in low-juvenile abundance years. For example, juvenile striped bass in very low-abundance years, when densities were below 0.02 individuals m^{-2} , attained >80% of potential consumption whereas only 70% was realized in moderate and high abundance years (Figure 5-10). The consumption deficit was greatest between early (July) and mid- summer (August). A strong relationship ($p < 0.05$) exists between p-values and abundance for the July through August period, while the generally negative relationship between p-values and abundance for the entire July through September period was not significant (Figure 5-10). The deficits in observed growth in weight in moderate- and high-abundance years (Figure 5-9) presumably result from limited per capita prey availability and reduced consumption levels by YOY striped bass.

Results from the growth rate, diet, and bioenergetics analyses all suggest that YOY striped bass experience more favorable feeding conditions and have higher consumption levels when age-0 striped bass abundance is low. The bioenergetics results strongly suggest that consumption supply (i.e. prey availability), rather than temperature, explained size differences in YOY striped bass among years. The relationship between p-values and juvenile abundance was negative and the data were fit best with a negative power function (Figure 5-10), similar to the relationships between juvenile abundance, length attained and growth rates (Figures 5-3 to 5-7).

Differences in benthic prey levels between the upper Bay and Potomac River may partly explain the failure to observe density-dependent growth in the Potomac. Benthic prey levels varied considerably among years in each system (Figure 5-11), but prey levels in the Potomac River were usually 3-4 times higher than levels in the upper Bay. Benthic prey levels reached $>8,000$ individuals m^{-2} in the Potomac River but were $>2,000$ m^{-2} during only one year in the upper Bay. The overall mean benthic prey abundance in the Potomac was $1,255$ m^{-2} compared to a mean level of 718 m^{-2} in the upper Bay (Figure 5-12).

The Holling Type II model, fit to the combined data for the upper Bay and Potomac River, described the relationship between YOY striped bass lengths in September and benthic prey level (Figure 5-13). The significant model fit ($p < 0.001$, $r^2 = 0.28$) predicted a maximum YOY striped bass length of 98.1 mm. The half-saturation constant K_m was 94.3 prey m^{-2} , indicating that a length of 49 mm is attainable at very low prey levels. There was considerable inter-annual variability in YOY lengths attained. The upper Bay and Potomac River benthic prey data were

conspicuously separated on this plot (Figure 5-13). Most of the Potomac observations were at prey levels above those where predicted lengths dropped appreciably. In contrast, upper Bay observations were mostly at low and intermediate prey levels where predicted striped bass lengths were declining relatively fast along the steep portion of the curve (Figure 5-13).

The frequency distributions of YOY striped bass growth rates in the upper Bay and Potomac were consistent with results of the analysis linking benthic prey level to length attained. Growth rates in the upper Bay were much more variable ($CV=0.73$) than in the Potomac River ($CV=0.30$). And, the mean growth rate in the upper Bay was lower (0.42mm d^{-1}) than in the Potomac (0.49 mm d^{-1}) (Figure 5-14a,c).

In a general linear model regression analysis to evaluate the relationship between growth rate and a selected suite of abiotic and biotic variables for the Potomac River and upper Bay (Table 5-5), only YOY striped bass abundance ($r=-0.32$) and per capita prey abundance ($r=0.31$) were significant ($p<0.05$) determinants of growth in the upper Bay. None of the six abiotic or biotic variables evaluated in the analysis were significantly related to growth in the Potomac River, a result consistent with other results reported in this chapter. Density dependence is important in regulating growth of YOY striped bass in the upper Bay but not in the Potomac River.

Mortality

Mean mortality rates of age-0 to age-1 striped bass between the first and second summer of life were similar in the upper Bay (0.008 d^{-1}) and Potomac River

(0.007 d⁻¹) (Figure 5-14b,d). The range and relative variability of mortality rates was similar between the upper Bay and Potomac (CV=0.27 and CV=0.25), while the distribution of mortality rates in the Potomac was more skewed to the right. .

A general linear model regression analysis of YOY striped bass mortality rates with respect to a suite of six abiotic and biotic variables was conducted for the Potomac River and upper Bay (Table 5-5). In the Potomac none of the variables was significant in explaining level of mortality. Mortality in the upper Bay was positively related to YOY abundance ($p<0.05$, $r^2=0.30$). And, the interaction effect between winter temperature and length attained in September was highly significant ($p<0.01$) in the upper Bay. This finding is important in explaining how density-dependent growth leads to size-selective overwinter mortality. Neither YOY length attained by September nor winter water temperature was a significant determinant of survival, but their interaction was significant ($p<0.01$) because the positive effect of YOY length attained became important for survival in years when winter temperatures were low. Results indicate that density-dependent mortality occurs during winter months, and that winter temperatures are an important regulator of abundance in the upper Bay but not the Potomac River.

Additional analyses were undertaken to evaluate density-dependent mortality in the upper Bay and Potomac River, leading to similar conclusions. A general linear model relating instantaneous daily mortality rate to age-0 striped bass abundance was significant in the upper Bay ($p<0.05$, $r^2=0.30$) but not in the Potomac. The positive relationship in the upper Bay indicated a density-dependent component of mortality (Figure 5-15). Results of a log-log unit slope test also were similar. In the upper Bay

the slope was <1 ($b=0.58$, $p < 0.01$), indicating density dependence while the slope in the Potomac ($b=0.78$) did not differ significantly from 1 (Figure 5-16).

Age-0 to Age-1+ Mortality and Recruited Abundance

The relative abundance of recruited year classes (age 3+) in gillnet collections varied among years in the upper Bay and Potomac River. I evaluated the average abundance of a year class across two- to three-year spans of ages of 3-4 and 3-5 years after fish recruit to the gillnet survey but had been vulnerable to fishing mortality for only 1-2 years. There was no relationship between age-0 abundance and the abundance of the same year class at ages 3 - 5 years (Figure 5-17a). There is a positive relationship between age-0 and age-1 abundance ($r^2=0.27$), suggesting a less than proportionate density-dependent increase in age-1 abundance as age-0 abundance increases (Figure 5-17b). The positive relationship between age-1 abundance and abundances at ages 3-4 ($r^2=0.50$, $p<0.05$) and 3-5 ($r^2=0.63$, $p<0.05$) are quite strong (Figure 5-17c,d). Overall, the observed relationships between age-0, age-1, and recruited-age abundances indicate that density-dependent processes regulate year-class strength of striped bass between age-0 and age-1 in the upper Chesapeake Bay.

A statistical model relating recruited abundances of striped bass at ages 3-5 to biotic and abiotic variables in upper Chesapeake Bay was developed that explains a substantial proportion of the observed inter-annual variability in year-class strength (Figure 5-18). Age-0 juvenile abundance and winter temperature experienced during the first year of life were included in the model because these variables represented

pre-recruit abundance, and included apparent larval mortality and a significant source of juvenile mortality beyond the pre-recruit stage (Table 5-5). Both age-0 abundance and winter temperature were significantly ($p < 0.001$) correlated with recruited abundance at ages 3-5, and the final model provided a good fit ($r^2 = 0.87$) to observed abundances at ages 3-5 years (Figure 5-18). The model was also run to predict abundances at ages 3-4 years but model fit declined ($r^2 = 0.43$) compared to the fit for ages 3-5 years. In the fit for ages 3-4, year-class data from 1998 could be included in the model and were responsible for the decreased model fit. The 1998 year class was initially large at age-0 in July and August. But, unlike most years in which abundances remained relatively constant through summer, YOY numbers in 1998 began to decline between August and September (Figure 5-9), potentially reducing the relative strength of this year class before the over-wintering period.

DISCUSSION

There is strong evidence of density-dependent growth and compensatory mortality at the age-0 juvenile stage in Chesapeake Bay striped bass. My results support the hypothesis that density dependence operates at the juvenile stage and contributes importantly to regulation of year-class strength. Density-dependent growth reduces age-0 juvenile growth rates and sizes-at-age, and smaller juveniles are at a greater risk for size-selective, over-wintering mortality. In general, recruitment processes consist of density-independent controls of larval survival, whereas juvenile

survival appears to result from both density-dependent juvenile growth and density-independent (i.e. winter severity) juvenile mortality.

Density-Dependent Growth

Density-dependent growth potentially is a primary mechanism underlying population regulation (Shepherd and Cushing, 1980). This hypothesis proposes that both larval-stage growth rate and time to reach a critical size, where mortality is substantially reduced are related to population density. The hypothesis provides a mechanism to explain the link between density-dependent growth and survival. However, in practice there is little direct evidence for a connection between density-dependent growth and survival during the larval stage (Cushing, 1981). A recent analysis evaluating density dependence in larval striped bass from the Potomac River was inconclusive (Rutherford et al., 2003). Consistent with other evaluations failing to identify density-dependent growth in larvae (Cowan et al., 2000), my results on larval-stage striped bass during 3 years in the upper Bay indicated the highest growth during 2003, a year of high larval abundance, and one of the strongest year classes during the past 2 decades (Chapter 2).

In contrast, density-dependent growth was detected at the juvenile stage in all but one of the six sub-populations of age-0 striped bass considered in this study. (Table 5-4, Figures 5-3 and 5-4). This finding is consistent with an investigation conducted decades ago that analyzed modal lengths of pre-recruit year classes before they migrated from Chesapeake Bay to predict future landings of striped bass in New

York waters (Austin and Hickey, 1978). In that study, the modal length of age-2 juveniles was small for large year-classes landed in New York, and the authors suggested that density dependence during the first few years of life might have been responsible. My results demonstrate that the strong density dependence in growth begins early in the juvenile stage, and I have proposed a mechanism to explain the relationship between year-class strength and juvenile size.

My results on age-0 striped bass resemble findings on density-dependence in juvenile salmonids and support the hypothesis that density-dependent effects on growth will be strongest at low to moderate abundance levels (Jenkins et al., 1999). A study on Atlantic salmon reported the greatest decline in juvenile lengths at low population densities (<1 individual m^{-2}) (Imre et al., 2005). Findings on density-dependent growth in 6 species and 11 populations of age-0 salmonids in Canadian streams revealed a similar pattern (Newman, 1993; Grant and Imre, 2005). Similarly, populations of brown trout from Rio Chaballos in northwestern Spain expressed density-dependent growth that was most pronounced in the low abundance range (Lobon-Cervia, 2005). A conceptual model provides a possible explanation for this pattern of density-dependent growth in a population of brown trout (*Salmo trutta*). The model assumes that optimal feeding sites are selected first and that as the number of trout increases, some individuals are forced to use suboptimal sites resulting in both decreased growth and increased variability in individual growth rates and lengths attained (Newman, 1993). When abundant, juvenile striped bass in Chesapeake Bay may be forced to feed in suboptimal habitats, at sites where benthic prey is less abundant.

Exploitative competition is a likely explanation for density dependence in growth of Chesapeake Bay striped bass since the relationship between length attained and abundance followed a negative power function (Table 5-4). Per capita benthic prey resources decline according to $1/\text{abundance}$ of predators (Kramer et al., 1997; Imre et al., 2005). In addition, the abundance levels of YOY striped bass at which density-dependent effects are most conspicuous appear to be too low for interference competition to be operating, an interpretation similar to that made on density dependence in juvenile salmonids (Grant and Imre, 2005).

Competition for food is a common explanation for density-dependent growth in juvenile fishes. Lekve et al. (2002) also proposed that prey abundance was limiting and responsible for density-dependent growth in juvenile Norwegian Skagerrak cod over the period 1919-1996. A caging experiment, testing for density-dependence in juvenile spot, *Leiostomus xanthurus*, detected up to a 97 percent reduction in growth and a 2-4-fold increase in mortality when densities were increased 5-fold (Craig et al., 2007). In that experiment, competition for food was evident and densities of benthic infauna at the end of the experiments were inversely related to spot density. Density-dependent effects on striped bass in my field research were less pronounced although clearly apparent. Density dependence in striped bass was significant but growth and mortality were less sensitive to changes in density than observed in the spot experiments.

While prey limitation appears to reduce growth of YOY striped bass in the upper Bay during high abundance years, there was no indication of density dependence in the Potomac River. The lack of density-dependent effects on growth in

the Potomac River stood in contrast with the remaining five systems that were compared. Age-0 striped bass from the Potomac River did not exhibit density-dependent reductions in length attained in September-October, or in growth rates. The abundance of benthic fauna that serve as prey was much higher in the Potomac River than in the upper Bay in all but one year from 1991-2003. It seems probable that benthic prey levels in the Potomac are above a threshold where prey-limited growth becomes important in most years, whereas prey levels in the upper Bay are consistently in the range where prey can be limiting.

The high benthic prey levels in the Potomac River suggest a more productive benthos than in the upper Bay. Higher nutrient loadings in the Potomac might explain the difference. Tsai et al. (1991) reported a positive relationship between nutrient loadings from a sewage treatment facility on the Potomac River and YOY striped bass production along a trophic gradient extending downriver from the facility. While those observations lend some support to a high nutrient loading, bottom-up argument, there has been little critical evaluation of how nutrient loadings may affect striped bass production and no evaluation of how it could contribute to density-dependent dynamics of YOY striped bass production.

Caveats and Interpretations

There is compelling evidence that density-dependent processes contribute significantly to observed growth and mortality patterns in YOY striped bass in some Chesapeake Bay nurseries. But, sampling artifacts and alternative explanations

potentially could lead to inappropriate conclusions regarding density-dependent growth and mortality. For example, small sizes of fish in high-abundance years might reflect delayed recruitment to the surveys rather than reduced growth rates in those years. It is unlikely that this alternative explains the small size of fish in high-abundance years. Seine-survey sampling commenced in July of each year, and YOY striped bass lengths during July were not related to abundance from 1989-2003.

Sampling artifacts due to density-dependent dispersal and catchability can be problematic in research attempting to isolate effects of density dependence on growth or mortality. Increased down-estuary dispersal by larger age-0 juveniles in wet, high-juvenile abundance years, and reduced sampling efficiency of yearlings the following year could have been partly responsible for apparent density dependence in growth and mortality reported here. For example, it is reported that yearling striped bass may disperse further down-estuary compared to the distribution of age-0 juveniles and may even move into coastal regions (Secor and Piccoli, 2007). I evaluated this possible sampling artifact by examining juvenile abundances and lengths from BITMAX mid-water trawl surveys at sites within and outside the primary nursery in October of 1996 and 2003 when age-0 juvenile abundances in the Bay were exceptionally high under wet hydrological conditions. If they existed, sampling artifacts due to density-dependent juvenile dispersal and down-estuary movements should have been evident during these two years. However, in both years there was a clear center of juvenile abundance within the usual primary nursery habitat, and no juveniles were collected below this sampling location (down-estuary of latitude = 39.2). Further, there was no

spatial trend ($p > 0.10$) in juvenile lengths in either 1996 or 2003, suggesting that there was no selective loss of larger individuals.

Dispersal loss of larger individuals in moderate and high abundance years does not explain the apparent density-dependent growth in YOY striped bass. The declines in attained lengths as a function of YOY abundance were consistent across five out of six distinct locations where surveys were conducted, and across three independent monitoring surveys and two different habitats (e.g. littoral versus deep channel) in the upper Bay. Further, the relationship between a year class' age-1 lengths in July was negatively ($p < 0.05$) related to its age-0 abundance (Figure 5-19) in the preceding year and is a projection of the relationship for age-0 juvenile abundance and age-0 lengths. The diminished lengths at age-1 followed the same negative relationship with abundance and growth rate observed for YOY fish. It is notable that size of YOY striped bass in September was unrelated to sizes in July, indicating that processes generating density-dependent growth are independent of YOY sizes early in the summer.

Apparent density dependence could derive from measurement error. To minimize this possibility, my analysis centered on the two most rigorously sampled locations in the Chesapeake Bay. This focus is no guarantee that density-dependent catchability did not occur, but my study had several advantages compared to others testing density dependence based on survey data. First, the analysis was on an anadromous species that is generally confined to the upper reaches of estuaries during its first year of life and exhibits strong preference for oligohaline and mesohaline salinities (0.5 to 15 salinities). Second, analyzing data from multiple surveys provided

length and abundance data from both littoral areas in the upper Bay and the adjacent deeper channel and downbay areas. In all years analyzed, there was a conspicuous center of YOY striped bass abundance located up-estuary of the most down-estuary extent of seine-survey and midwater-trawl sampling in the Bay. If there had been density-dependent dispersal into peripheral habitats, there would have been a disproportionate increase in catches from deeper channel areas and further downbay. There was no indication of such increases (Figure 5-19). Rather, the ratio of catches in the midwater trawl survey in deeper channel waters and including locations further downbay to the catches in the seine survey in littoral habitat (Figure 5-19) were similar in a high abundance year (e.g., 2003) and a low abundance year (e.g., 2002) (approximately 150 to 1).

Consumption Demand, Availability of Benthic Prey, and Bioenergetics

Consumption demand of YOY striped bass may exceed supply during moderate and high abundance years. During the years covered by my research, 1989-2003, maximum YOY densities at some stations reached 0.47 m^{-2} in the upper Bay during summer, and mean benthic prey densities were 674 m^{-2} . Polychaetes and amphipods were the dominant taxa in benthic samples from 2003, as well as in gut contents of juvenile striped bass in that year. The approximate wet weights of polychaetes and amphipods within the size range (4-7 mm) consumed by juvenile striped bass in this study were approximately 0.07 and 0.13 mg for amphipods and polychaetes, respectively, based on reported length-weight relationships (Rose et al.,

1996) . Thus, 0.07 g m^{-2} of these benthic prey types would be available to striped bass in the high striped bass abundance year 2003, assuming equal proportions of each prey type and that sizes of prey consumed by juveniles were representative of the size distribution of prey available. Population-level consumption demand of striped bass juveniles reached $0.08 \text{ g m}^{-2} \text{ d}^{-1}$ at the highest density locations in 2003, i.e., exceeding available standing stock (Figure 5-9). Typical turnover rates for amphipod and polychaete prey are 0.1 d^{-1} and 0.05 d^{-1} , respectively (Shaughnessy and Holland, 1989), and corresponding doubling times are 6.9 and 13.8 days. Thus, the estimated consumption demand could not be sustained without frequent movements by juvenile striped bass to different locations. The model result suggests that prey limitation is likely in the upper Bay during years of high YOY striped bass abundance.

I hypothesized that population-level consumption represents a significant fraction of available benthic prey to YOY striped bass. Actual consumption demand is undoubtedly higher than my estimated value since gear efficiency of seines used to sample juvenile striped bass may only approach 60 percent (Weinstein and Davis, 1980). Conceivably, YOY striped bass abundance and population consumption could be twice the level reported here. In addition, age-0 striped bass coexist with many other fishes in Chesapeake Bay that are at least partly benthivorous, including white perch, hogchoker, gobies, and ictalurid catfishes. The combined consumption demand of these species has a strong potential to locally exceed benthic prey supply during years when abundance of YOY striped bass is high. Correlated recruitments of anadromous species including striped bass, white perch, and river herrings that are linked to climatology (Wood, 2000) will increase competition for limited benthic prey

resources in favorable years. A more rigorous evaluation of inter-annual differences in benthic prey availability and striped bass population demand in other tributaries of the Bay is needed. Such an evaluation should address uncertainties in benthic prey sampling efficiency, prey equilibrium densities and turnover rates, prey sizes and caloric densities, as well as the demands of other competing benthivores.

The bioenergetics results, along with the growth-abundance relationship, suggested prey-limited growth of YOY striped bass in the upper Bay during most years. Results indicated that differences in temperatures between years did not explain or account for inter-annual differences in growth of YOY striped bass in the Bay. Observed growth of YOY striped bass was below growth potential in all years except 1995 and 2002, years of low YOY abundance. My conclusion is consistent with that of an earlier bioenergetics analysis of growth potential in juvenile Chesapeake Bay striped bass (Hartman and Brandt, 1995). The Hartman and Brandt analysis, based on a single year's data, concluded that prey availability limited consumption and growth of juveniles. Results reported here, based on 15 years of data in the upper Bay, indicated a deficit in prey consumption for most years in the 1989-2003 period.

Mortality

Juvenile mortality has been analyzed in other populations of striped bass (Dorazio et al., 1991; Buckel et al., 1999; Kimmerer et al., 2000). A tagging study focused on age-0 juvenile striped bass mortality in the Patuxent River estimated juvenile mortality rates of 0.03 d^{-1} (Dorazio et al., 1991). The higher rates in the

Patuxent River (0.03 d^{-1}) compared to rates in my study (0.003 d^{-1} to 0.012 d^{-1}) may have been a result of the Patuxent study focusing exclusively on mortality during earlier juvenile life between June and September, while my estimates were averaged over the entire first year of life. Mortality rates of age-0 juvenile striped bass in the San Francisco estuary also were higher than those reported here from the upper Chesapeake Bay (Kimmerer et al., 2000). The highest mortality rates reported here were similar to the lowest rates in the San Francisco estuary.

YOY striped bass experience density-dependent mortality in addition to density-dependent growth in upper Chesapeake Bay. Differences in density-dependent mortality in high- versus low-abundance years could have a significant effect on regulation of recruitment level. For example, in low-abundance versus high-abundance years, mortality rates were approximately 0.006 d^{-1} and 0.009 d^{-1} , respectively (Figure 5-15). Juvenile striped bass exposed to these rates would experience a 3-fold difference in cumulative survival rates during the first year of life. This implies that observed abundance levels varying >10-fold in age-0 fish potentially can be reduced to 3-4-fold differences through effects of compensatory mortality by the time a year class recruits to the fishery at age 3.

There was no evidence of density-dependent mortality for YOY striped bass in the Potomac River. One explanation, in addition to the high benthic prey levels in the Potomac, is the relatively few years when juvenile abundance was below $0.01 \text{ juveniles m}^{-2}$ (Figure 5-3). Density-dependent effects in all other populations in the Bay were most evident at low to moderate levels of juvenile abundance ($<0.01 \text{ m}^{-2}$). Juvenile abundances in the Potomac exceeded these low levels in most of the years

analyzed (1991-2003). The result is reminiscent of the failure to detect density-dependent growth in brown trout (Elliott, 1990) in a habitat that supported high trout densities with limited contrast in densities.

Regulation of Recruitment

Growth and mortality of age-0 juveniles can be density-dependent and have the potential to regulate recruitments of striped bass in upper Chesapeake Bay and other Bay subpopulations. In the Hudson River, size-dependent over-winter mortality (Hurst and Conover, 1998) and density-dependent predation mortality (Buckel et al., 1999), that presumably also is size-dependent, were reported. No direct link between density-dependent growth and survival was reported in YOY striped bass from the Hudson River. Detecting mechanisms for density-dependent regulation is difficult in the field but effectively demonstrated in experimental research. For example, experiments on spot reported reduced growth and survival at elevated spot densities and highlighted a mechanism for recruitment regulation via density-dependent competition for benthic prey (Craig et al., 2007). Field research on plaice (Zijlstra et al. 1982) and Norwegian cod (Fromentin et al., 2001; Lekve et al., 2002) has provided evidence for a direct connection between growth and mortality processes, indicating that the linked processes can be a strong regulator of recruitment.

Relationships reported herein were easily detected in the monitoring data sets and it is surprising that they were not recognized previously, given the importance of the Chesapeake Bay population to the striped bass fishery. Research on Chesapeake

Bay striped bass recruitment has a long history and, to my knowledge, only one earlier study recognized density-dependent growth in Chesapeake Bay striped bass (Austin and Hickey, 1978). One simple explanation for the lack of earlier reports is simply the increasing availability of data in multi-decadal time series that now include strong contrasts in recruitment levels. A review of compensatory density dependence in fish populations (Rose et al., 2001) includes the noteworthy quote by (Turchin, 1995), who states, "...all empirical analyses agree that the frequency of detecting density dependence increases with the length of the data series. Thus, most field populations are regulated, and previous failures to show this were owing to inadequate data sets..."

In years of high abundance in upper Chesapeake Bay and some tributaries, a large portion of the population could be at risk to over-wintering mortality. Striped bass cease feeding at temperatures $<10^{\circ}\text{C}$ (Hurst and Conover, 2001) and must rely on energy reserves to survive through winter. Larger individuals at a higher nutritional condition level would have a survival advantage. This is a likely mechanism to explain results reported here. However, other sources of size-dependent juvenile mortality, such as predation, may be important and were not considered in my research.

The recruitment process is described by a combination of environmental controls over larval survival and density-dependent constraints on juvenile survival. Spawner abundance controls egg production but most inter-annual variability in age-0 abundance is generated by stochastic environmental variability (Polgar, 1981). Environmental controls that generate this variability in early life were

discussed in Chapters 1- 4 of my dissertation and also in earlier research on striped bass recruitment variability (Cowan et al., 1993; Secor and Houde, 1995; Rutherford et al., 1997; North and Houde, 2003). In years with moderate to high age-0 juvenile abundances, juvenile growth and size-at-age are reduced and this places juveniles at a greater risk for size-selective over-wintering mortality. Juvenile survival depends on the interaction between density-dependent juvenile growth and a density-independent sources of juvenile mortality. Other studies on recruitment variability recognized the complex interplay between density-independent and density-dependent survival in the recruitment process. For example, the number of largemouth bass surviving the first year of life in a northern lake (Michigan, USA) was a result of complex interactions among adult demographics, size-selective predation, and over-winter mortality (Post, 1998).

A Paulik diagram (Paulik, 1973) can be used to conceptualize the recruitment process of striped bass in upper Chesapeake Bay based on findings reported in this chapter (Figure 5-20). Paulik's approach describe the dynamics of populations exhibiting density-independent and density-dependent relationships among life stages (Rothschild, 2000; Nash and Dickey-Collas, 2005). In striped bass, it is the transition from age-0 to older age classes (age 3+) that appears to be density dependent in most sub-populations in Chesapeake Bay and, as such, serves as to regulate levels of recruitment. Similarly, "coarse and fine controls" have been used to describe the recruitment process in North Sea plaice (Van der Veer et al., 2000).

Detection of density dependence in a population and enhanced understanding of the underlying process can potentially foster more effective management of the

striped bass resource. For example, the level of age-0 abundance measured by juvenile recruitment surveys is positively but not significantly related to recruited abundance at ages of 3-5 years as detected in gillnet surveys in upper Chesapeake Bay. Mean instantaneous daily mortality rates of age-0 striped bass varied more than 2-fold from 1989-2003 in the upper Bay. Differences in mortality at that level have the potential to result in 3-fold reductions in year-class variability when they operate during late summer to over-winter in YOY striped bass. My forecasting model (Figure 5-18) included both age-0 abundance, an outcome most sensitive to biophysical controls on larval survival, and winter temperature to account for size-selective over-wintering juvenile mortality. The model provided a very good fit ($r^2=0.87$) to recruited abundances at ages 3-5 years, and surpassed age-0 abundance alone as an indicator of recruited year-class strength (Figure 5-17).

Findings reported here offer new insight into mechanisms controlling and regulating recruitment of striped bass and potentially other anadromous fishes. A re-evaluation or re-casting of existing individual-based models of striped bass recruitment (Cowan et al., 1993), and development of new models that include density-dependent effects on growth and survival would be timely and important. My findings could be used to improve capabilities of recruitment forecasting models.

The findings in this chapter also have implications for explaining and understanding dynamics and resilience of the North Atlantic striped bass population. The rapid recovery of Atlantic Coast striped bass, after a moratorium was enforced in the mid 1980s, may have been abetted by a compensatory reduction in juvenile mortality rates and increased reproductive rates (i.e. recruits/spawner) under reduced

abundance. Other research and stock assessments indicate that Atlantic coast striped bass spawning stock biomass and recruitments fit modified Ricker-type stock-recruitment models, if the models include appropriate environmental variables (North and Houde, 2003). Recruitment of striped bass is only weakly coupled to spawning stock biomass alone. Larval-stage survival is controlled by environmental factors and is density independent. Density-dependent compensation is strong in the juvenile stage. Findings in this chapter provide analysis and a plausible mechanism to explain recruitment variability in striped bass, and they provide a framework to develop forecasting capability.

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Table 5-1. Striped bass juvenile surveys, Chesapeake Bay and tributaries. Locations where growth of young-of-the-year fish was estimated and the data sets and methods used for analysis. Time periods represent the longest consecutive period when there were no major changes in stations sampled at each location.

Location	Parameters	Data Sources	Time Period	Method
Maryland				
Upper Bay	length attained	MD DNR recruitment survey	1980-2003	mean length in September
	length attained	NSF BITMAX research	2001-2003	mean length in October
	growth rate	MD DNR recruitment survey	1980-2003	difference in median length
	growth rate	NSF BITMAX research	2001-2003	modal progression
Potomac River	length attained	MD DNR recruitment survey	1991-2003	mean length in September
	growth rate	MD DNR recruitment survey	1991-2003	difference in median length
Nanticoke River	length attained	MD DNR recruitment survey	1980-2003	mean length in September
Virginia				
James River	length attained	VIMS recruitment survey	1982-2003	mean length in September
		VIMS recruitment survey	1982-2003	
York River	length attained	VIMS recruitment survey	1982-3003	mean length in September
Rappahannock	length attained	VIMS recruitment survey	1988-2003	mean length in September

Table 5-2. Striped bass juvenile surveys that provided data for mortality estimation. Locations, data sources and time periods are given. Time periods represent the longest consecutive period when all stations were sampled at each location for all years.

Location	Parameter	Data Source	Time Period
Maryland			
Upper Bay	Daily instantaneous mortality rate	MD DNR recruitment survey	1989-2003
Potomac River	Daily instantaneous mortality rate	MD DNR recruitment survey	1991-2003

Table 5-3. Young-of-the-year striped bass, upper Chesapeake Bay: mean annual density (no. m⁻²) and maximum density (no. m⁻²) among all sites during July, August, and September, and mean length attained (mm) by September from MDDNR recruitment surveys, 1989 through 2003.

Year	Mean Density	Max. Density	Mean length Attained
1989	.036	.163	77.5
1990	.008	.044	84.7
1991	.008	.085	82.8
1992	.003	.028	104.5
1993	.045	.444	87.2
1994	.036	.203	67.8
1995	.009	.060	96.1
1996	.046	.313	83.2
1997	.016	.099	77.7
1998	.016	.131	85.8
1999	.006	.051	96.8
2000	.024	.157	76.3
2001	.030	.160	93.3
2002	.004	.025	84.8
2003	.081	.471	79.6

Table 5-4. Striped bass young-of-the-year: abundance vs length relationships in Chesapeake Bay and tributaries. Relationship between length attained at the end of the growing season and abundance (no. m⁻²) for major subpopulations of striped bass juveniles, 1980-2003. Comparison between negative power and linear model fits are shown. The negative power model fit best in each case. Comparison of parameter estimates between Maryland and Virginia subpopulations is not possible because Maryland abundance is reported as no. m⁻² and Virginia as catch per unit effort.

Location	Linear Model	Negative Power Model
Maryland		
Upper Bay	b=-234.7, r ² =0.24, p<0.01	b=-0.08, r ² =0.61, p<0.0001
Nanticoke River*	b=-175.3, r ² =0.18, p<0.05	b=-0.05, r ² =0.32, p<0.01
Potomac River	N.S.	N.S.
Virginia**		
James River	b=-243, r ² =0.40, p<0.001	b=-0.12, r ² =0.48, p<0.001
York River	b=-487, r ² =0.20, p<0.05	b=-0.15, r ² =0.34, p<0.01
Rappahannock	b=-280, r ² =0.18, p<0.1	b=-0.16, r ² =0.40, p<0.01

* Only 4 stations sampled consistently during 1980-2003

** Abundance at Virginia locations estimated using average area swept in most recent years

Table 5-5. Relationship from linear regression between selected environmental variables and YOY striped bass growth and mortality in upper Chesapeake Bay and the Potomac River for 1989-2003 and 1991-2003, respectively. All data were log-transformed prior to testing and the coefficient estimate is in log_e units. Significant effects are indicated in bold typeface. NS = not significant.

Response	Variable	Mult. R ²	Coefficient	p
Growth				
Upper Bay	Summer salinity			N.S.
	Summer temperature			N.S.
	Summer dissolved oxygen			N.S.
	Juvenile Striped Bass abundance	0.35	-0.32	<0.05
	Benthic Prey Abundance			N.S.
	Per capita prey abundance	0.27	0.31	<0.05
Potomac	Summer salinity			N.S.
	Summer temperature			N.S.
	Summer dissolved oxygen			N.S.
	Juvenile Striped Bass abundance			N.S.
	Benthic Prey Abundance			N.S.
	Per capita prey Abundance			N.S.
Mortality				
Upper Bay	Summer salinity			N.S.
	Summer temperature			N.S.
	Juvenile Striped Bass Abundance	0.30	0.17	<0.05
	Mean length in September			N.S.
	Winter temperature			N.S.
	Winter salinity			N.S.
	Mean length x Winter temperature	0.62	-16.1(length), -5.0(temp.) 3.7 (interaction)	<0.01
Potomac	Summer salinity			N.S.
	Summer temperature			N.S.
	Juvenile Striped Bass Abundance			N.S.
	Mean length in September			N.S.
	Winter temperature			N.S.
	Winter salinity			N.S.
	Mean length x Winter temperature			N.S.

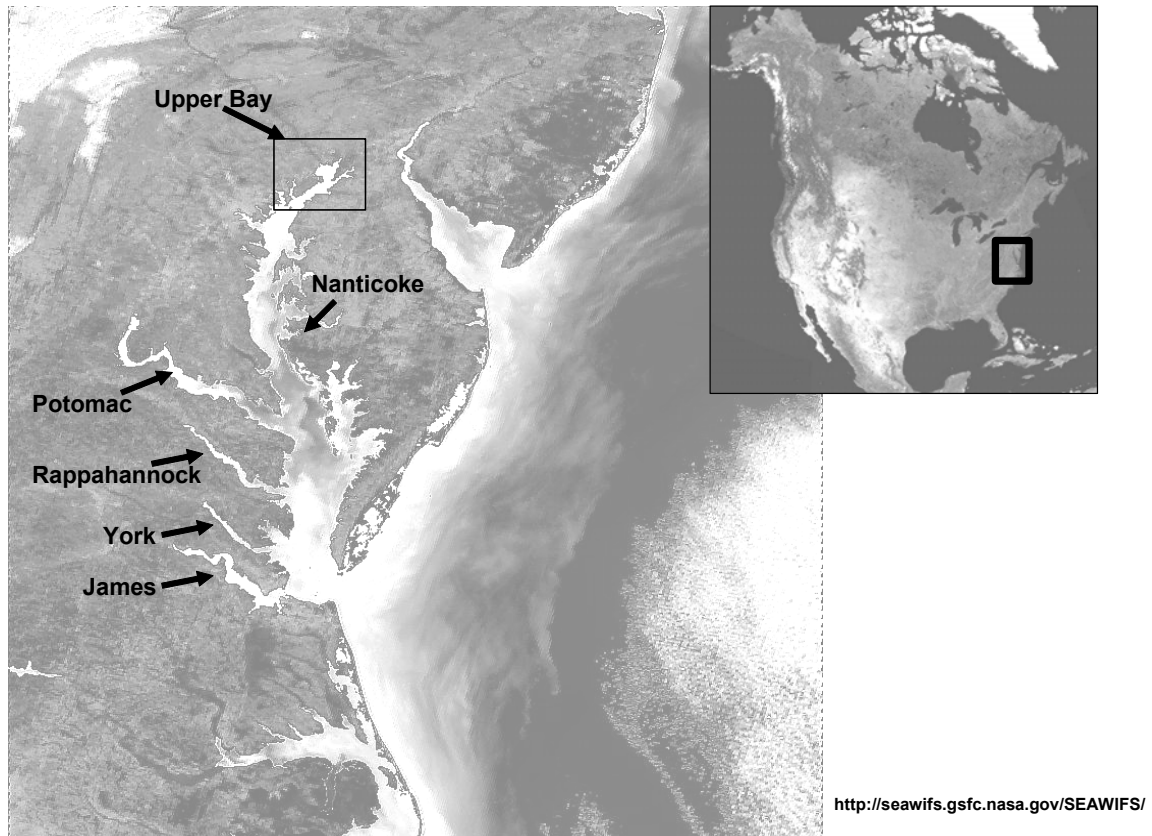


Figure 5-1. Map of study locations in Chesapeake Bay. Arrows indicate major striped bass spawning areas in the Bay where long-term juvenile recruitment monitoring was conducted at consistent sampling stations for at least 10 years.

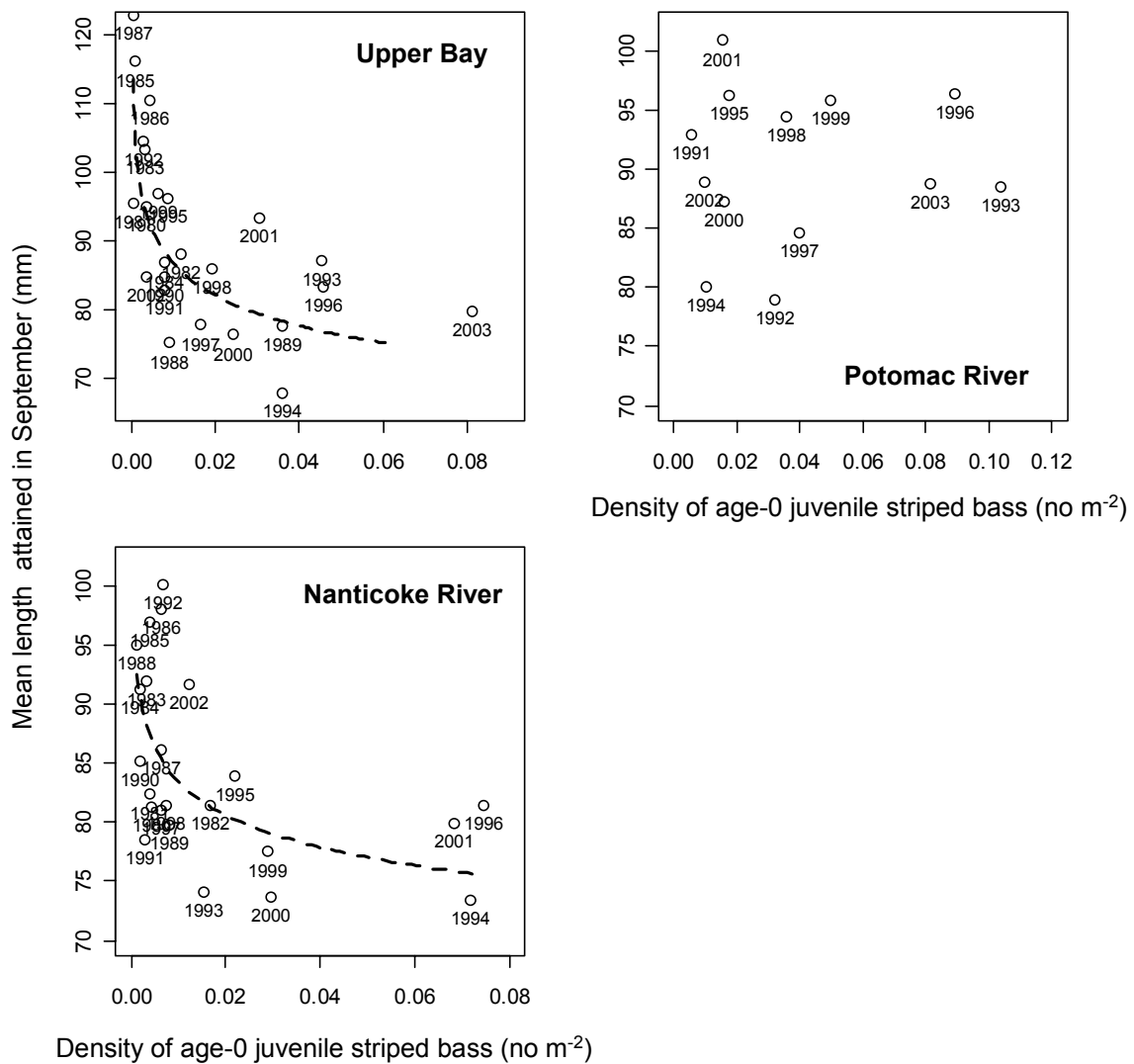


Figure 5-2. Relationship between the abundance and length attained at the end of the first growing season for age-0 striped bass in upper Chesapeake Bay during BITMAX, 2001-2003. The solid line within boxplots represents the median total length (mm), the lower and upper boundaries of boxes represent the 25th and 75th percentiles of length, and the lower and upper whiskers represent the minimum and maximum lengths unless outliers are present. The black dots are outliers.

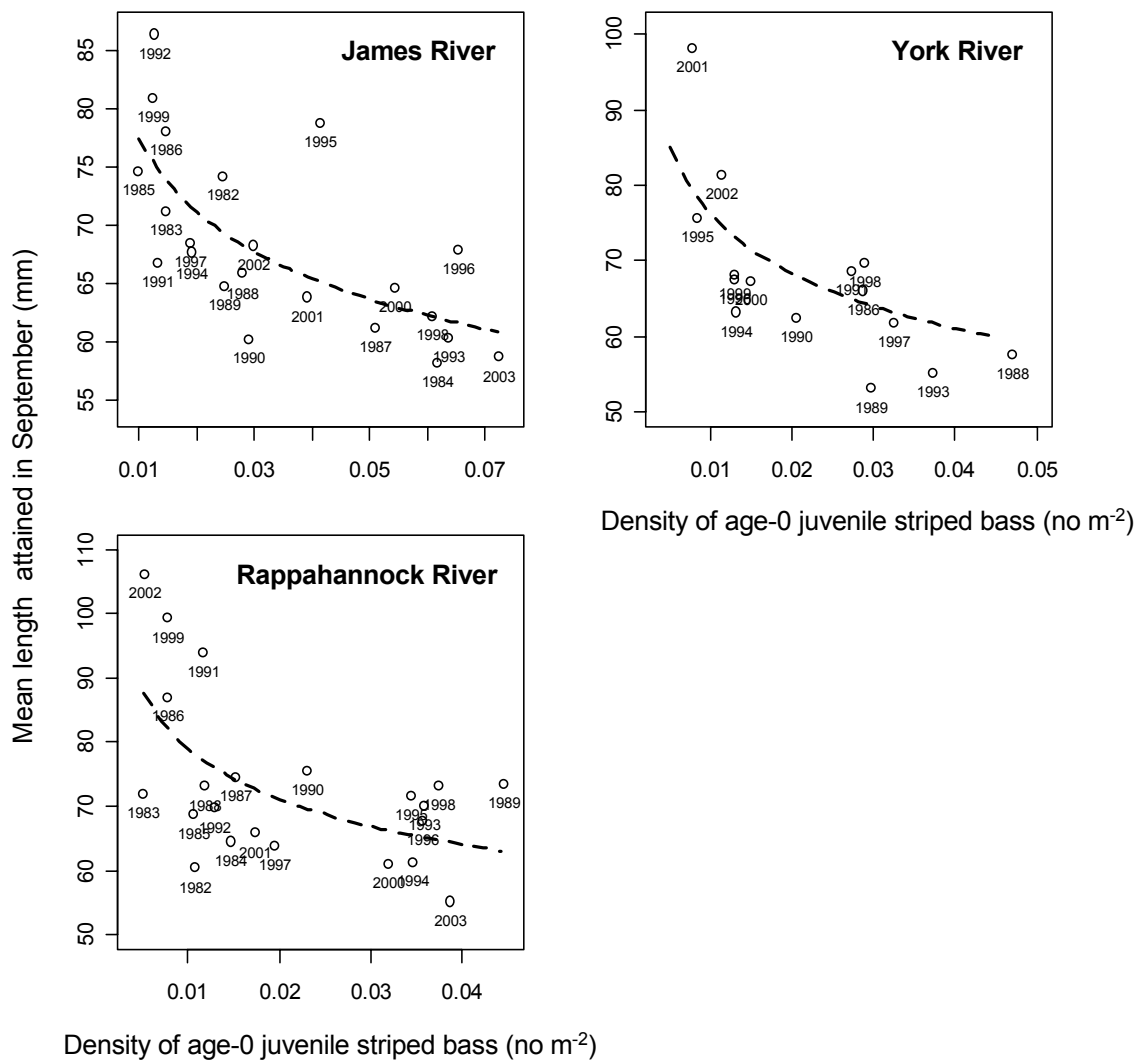


Figure 5-3. Relationship between the abundance and length attained at the end of the first growing season (September) for age-0 striped bass in upper Chesapeake Bay, the Nanticoke River, and Potomac River, Maryland. Derived from MDDNR seine-survey data. Dashed lines are the fitted power models (Table 5-4).

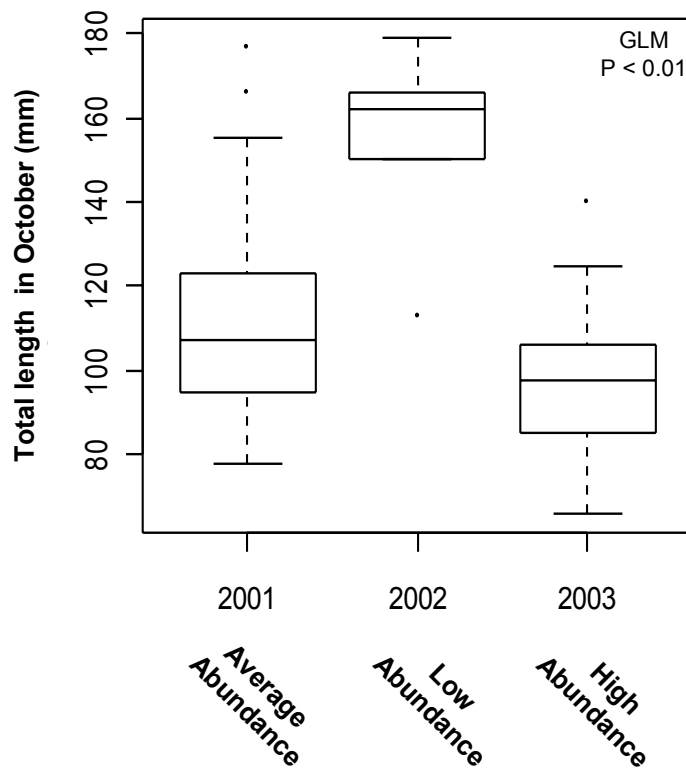


Figure 5-4. Relationship between the abundance and length attained at the end of the first growing season (September) for age-0 striped bass in the James River, York River, and Rappahannock River, Virginia; 1980-2003 for the James and York Rivers, 1986-2002 for the Rappahannock River. Derived from VIMS seine-survey data. Dashed lines are the fitted power models (Table 5-4).

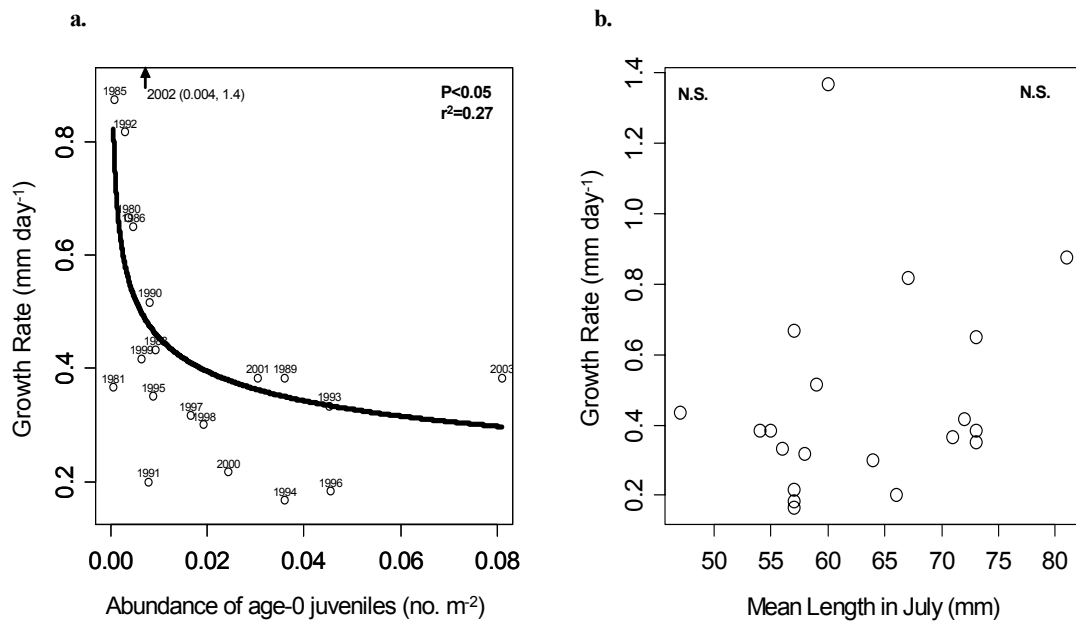


Figure 5-5. Upper Chesapeake Bay, YOY striped bass. Relationship between; a) summer growth rates and age-0 juvenile abundance in September and b) relationship between growth rates and mean length in July. Growth rates were based on differences between August and September median lengths from MDDNR seine collections in upper Chesapeake Bay, 1980-2003.

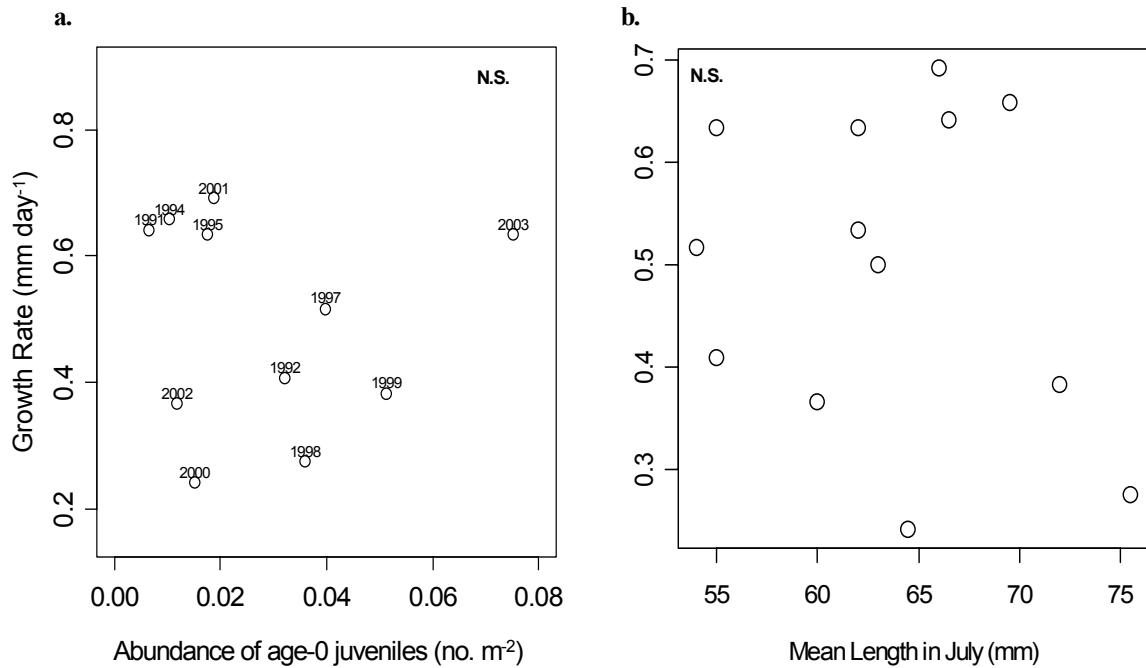


Figure 5-6. Potomac River, YOY striped bass. Relationship between: a) summer growth rates and age-0 juvenile abundance in September and b) growth rates and mean length in July. Growth rates were based on differences between August and September median lengths from MDDNR seine collections in the Potomac River, 1991-2003.

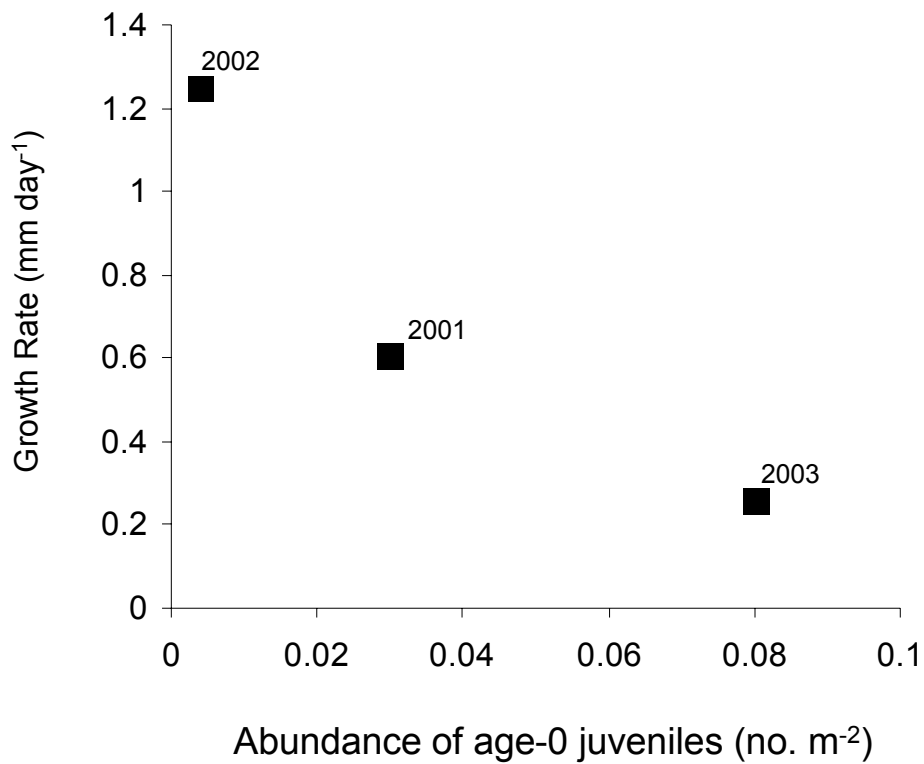


Figure 5-7. Upper Chesapeake Bay, YOY striped bass. Relationship between growth rates based on modal length progression and age-0 juvenile abundance in July, based on BITMAX midwater trawl collections from the main channel of upper Chesapeake Bay in 2001, 2002, and 2003.

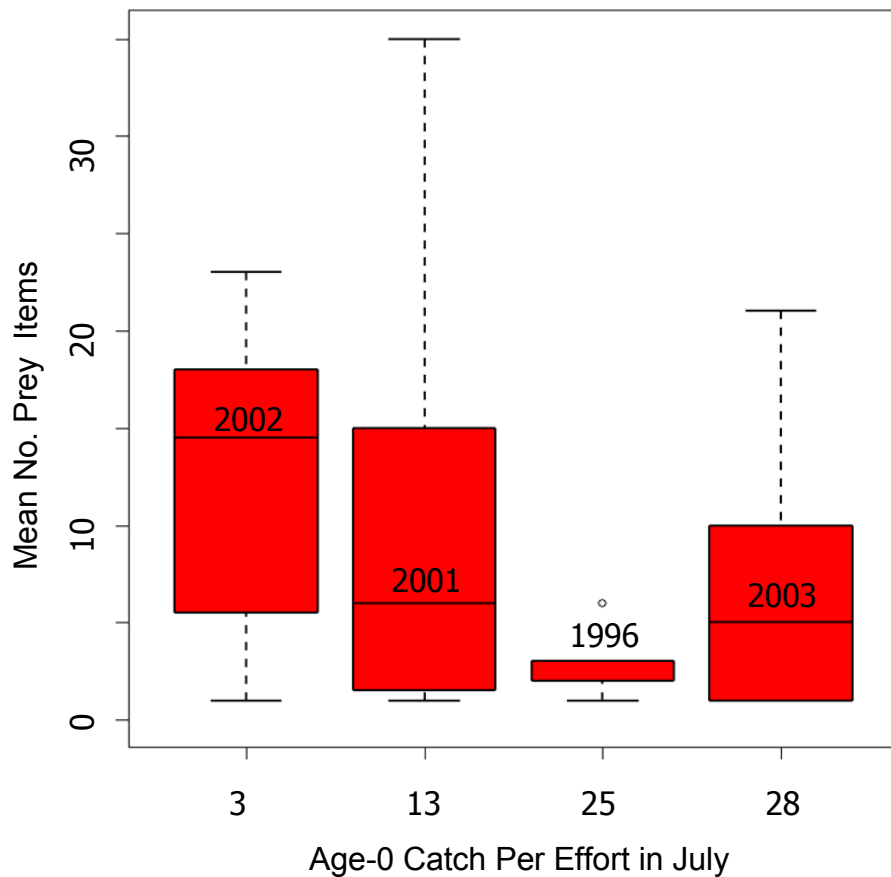


Figure 5-8. Feeding Success. Boxplots showing the distribution of the number of prey consumed by Age-0 juvenile striped bass in the upper Chesapeake Bay based on striped bass trawled in July from NSF TIES (1996) and BITMAX research cruises. The solid line within boxplots represents the median number of prey items in juvenile guts, the lower and upper boundaries of boxes represent the 25th and 75th percentiles of prey number, and the lower and upper whiskers represent the minimum and maximum prey numbers.

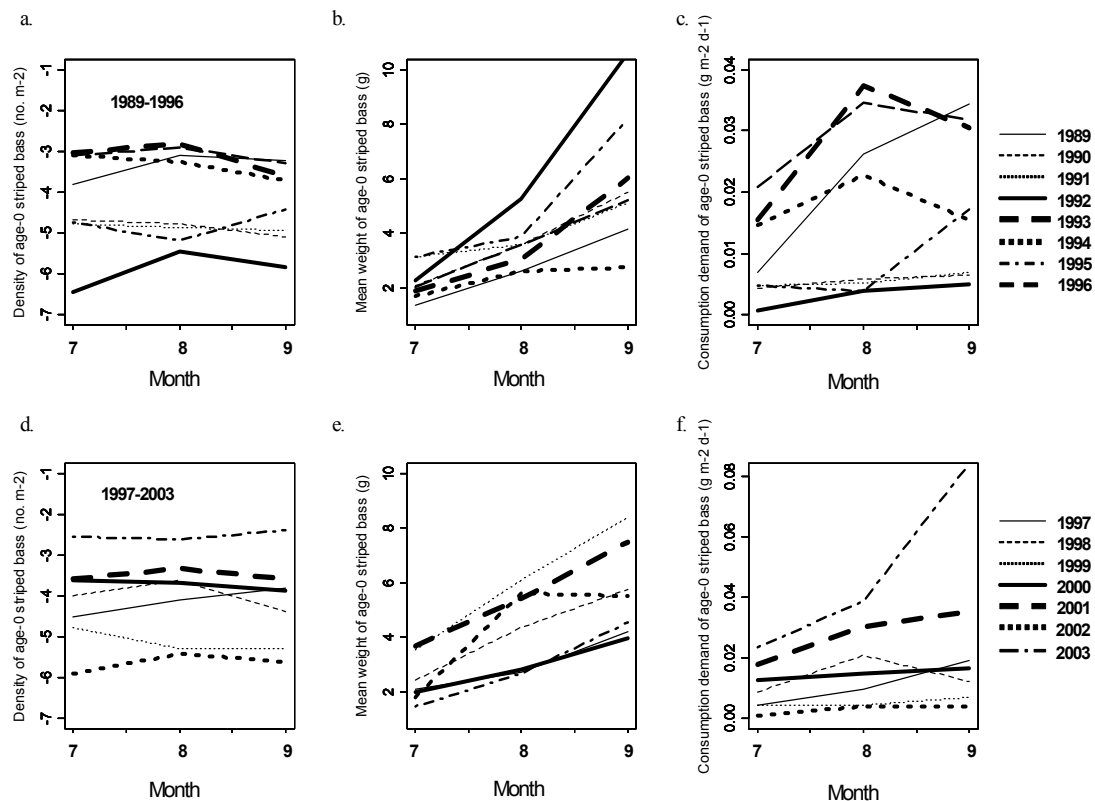


Figure 5-9. Mean density, mean individual wet weight, and population consumption demand of age-0 striped bass in upper Chesapeake Bay in July, August, and September for the years 1989 through 1996 (a through c) and 1997 through 2003 (d through f).

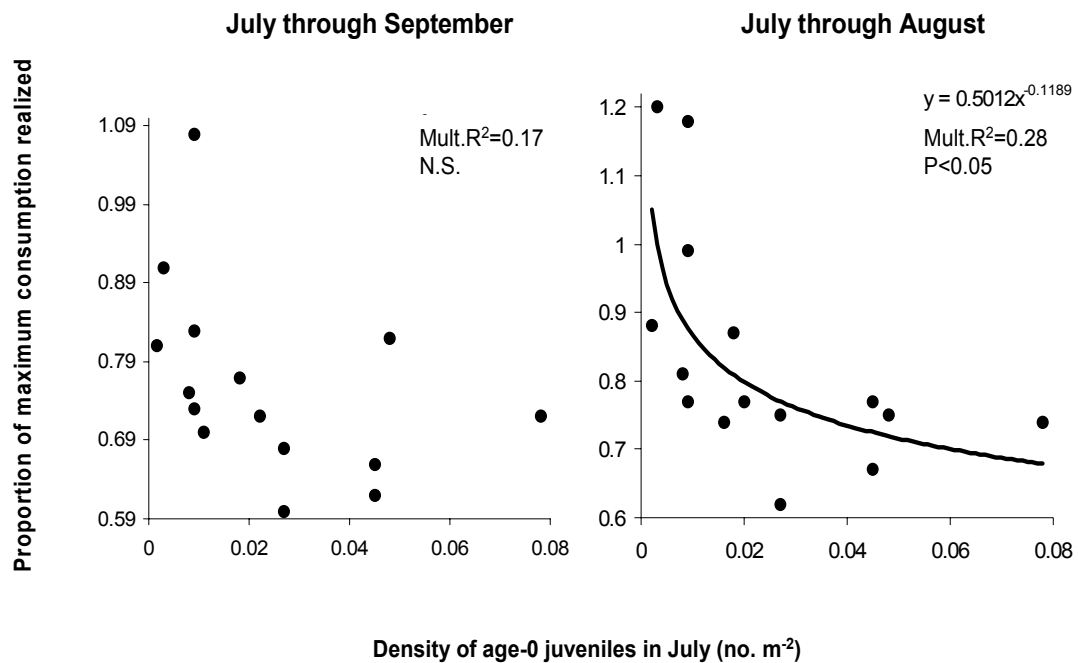


Figure 5-10. Relationship between the proportion of consumption demand realized and juvenile striped bass abundance in upper Chesapeake Bay for the periods July through September and July through August for the years 1989 through 2003.

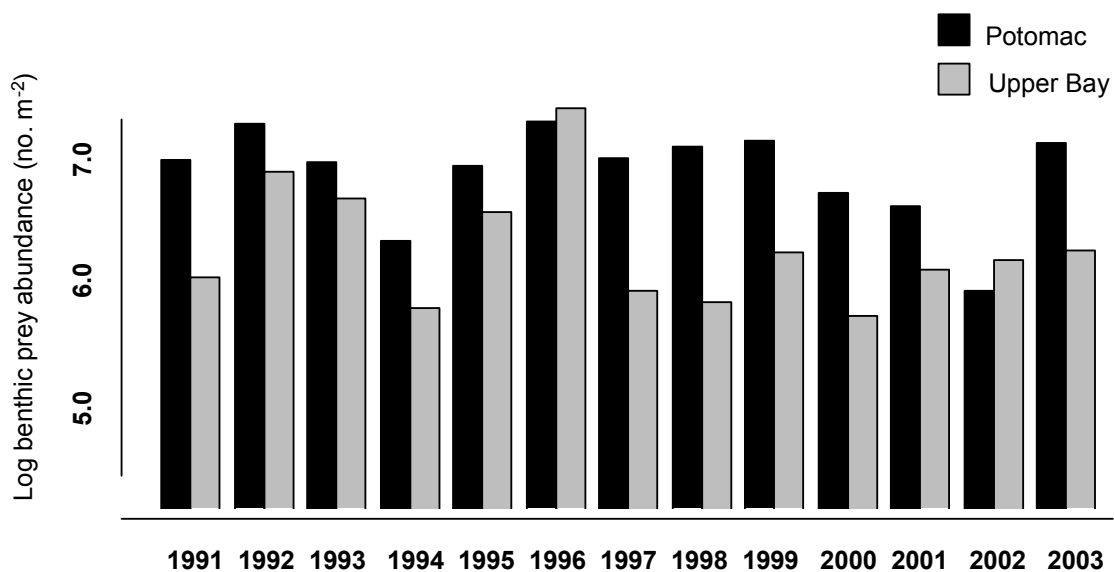


Figure 5-11. Benthic prey levels. Log_e mean annual abundance of benthic fauna in the upper Chesapeake Bay and Potomac River during late summer for the years 1991 through 2003.

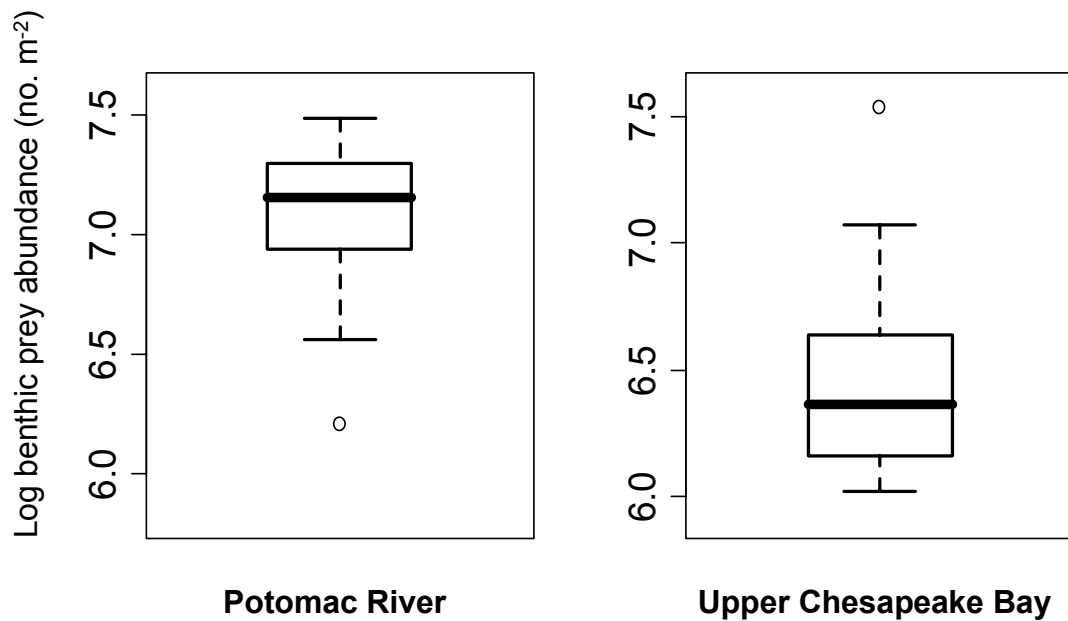


Figure 5-12. Benthic prey levels. Boxplots showing distribution of annual levels of benthic prey abundances in the Potomac River and upper Chesapeake Bay during late summer for years 1989-2003. The solid line within boxplots represents the loge median benthic prey density (no. m⁻²). The lower and upper boundaries of boxes represent the 25th and 75th percentiles of prey density, and the lower and upper whiskers represent the minimum and maximum prey densities unless outliers are present. Open circles are outliers.

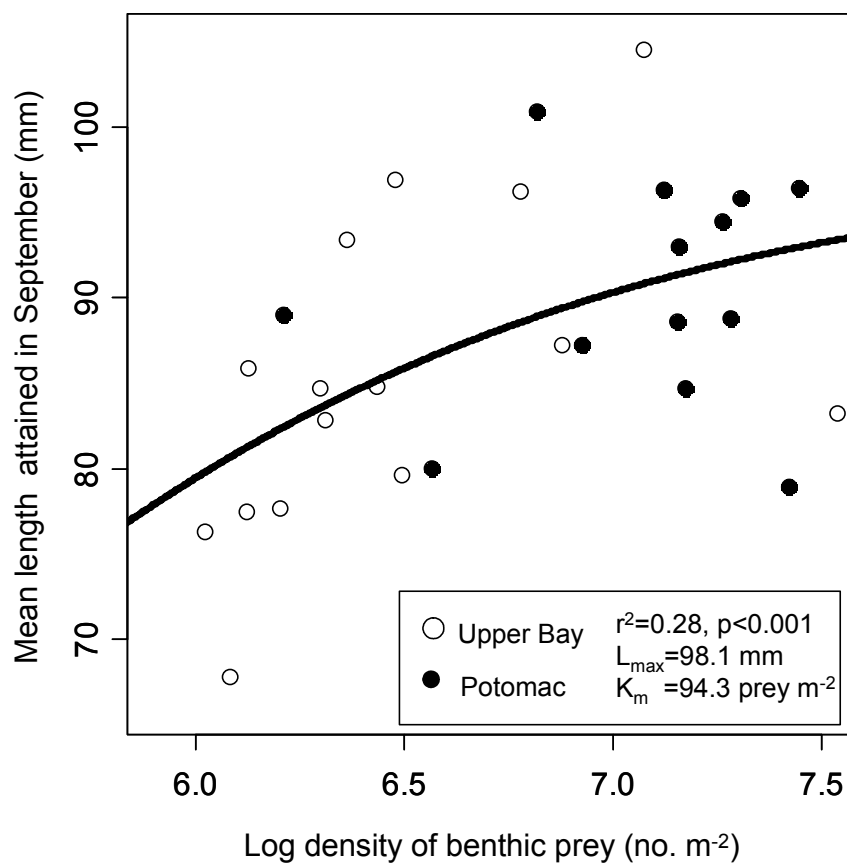


Figure 5-13. Relationship between the mean length attained by age-0 juvenile striped bass and the mean annual abundance of benthic fauna in the upper Chesapeake Bay and Potomac river. A Holling Type II model was fit to the observed juvenile lengths and untransformed benthic prey data. Parameter estimates are for untransformed data but the observed and predicted model outputs are plotted against \log_e benthic prey density.

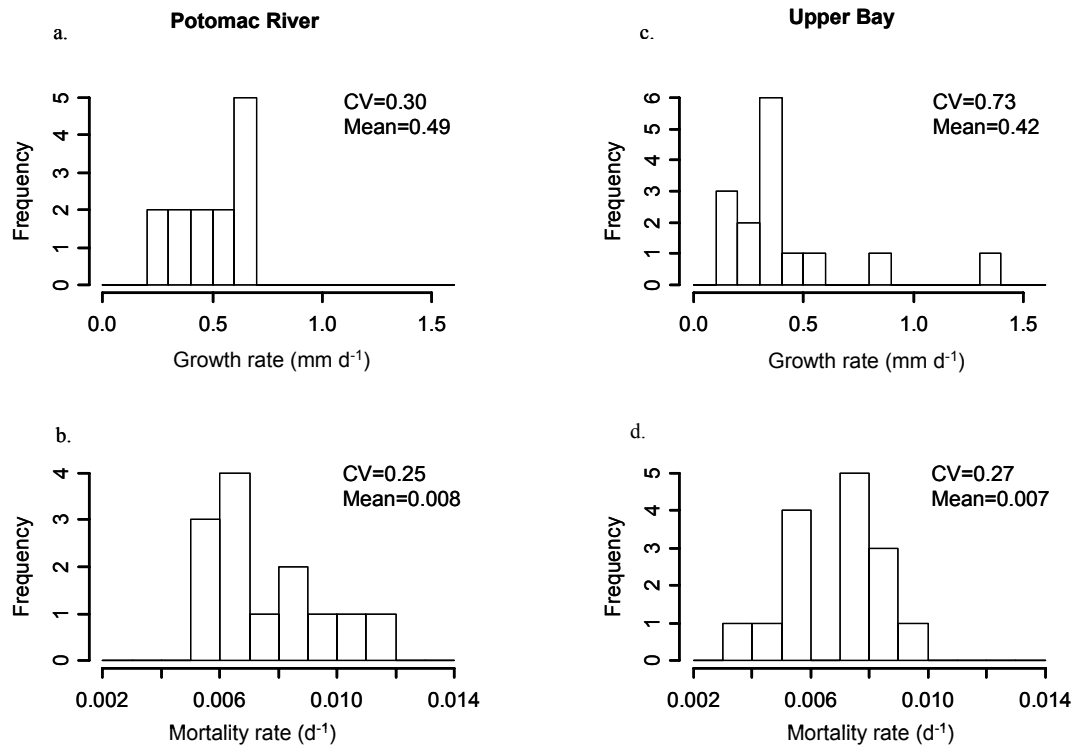


Figure 5-14. Growth rates of YOY striped bass from a) the Potomac River and c) upper Chesapeake Bay and mortality rates from b) the Potomac River and d) upper Chesapeake Bay

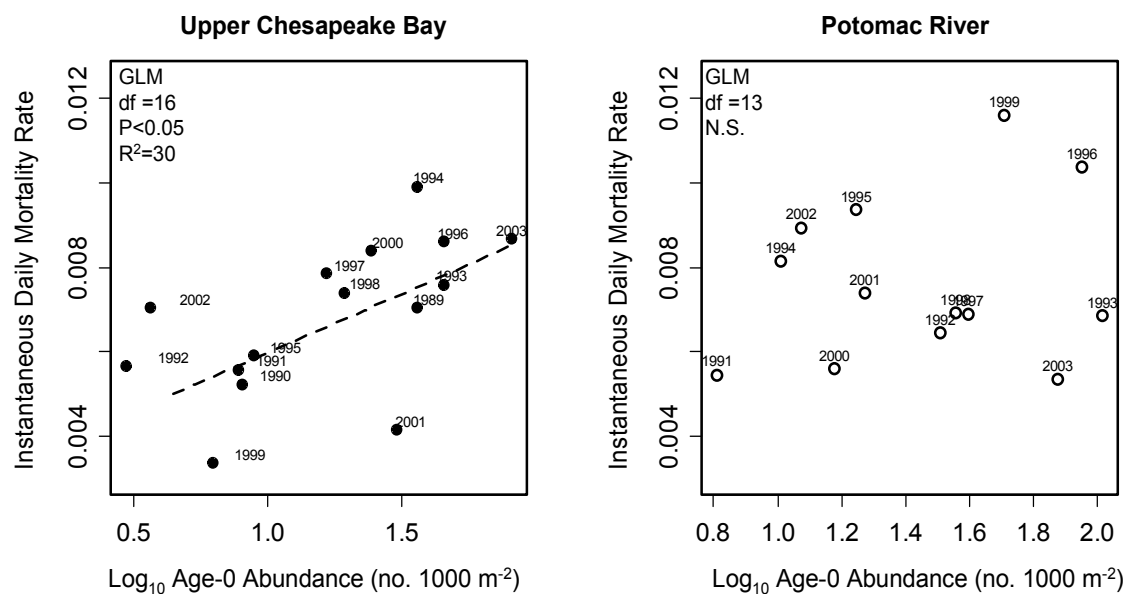


Figure 5-15. Relationship between age-0 striped bass abundance and instantaneous daily mortality rate (d⁻¹) for upper Chesapeake Bay 1989-2004 and the Potomac River 1991-2003.

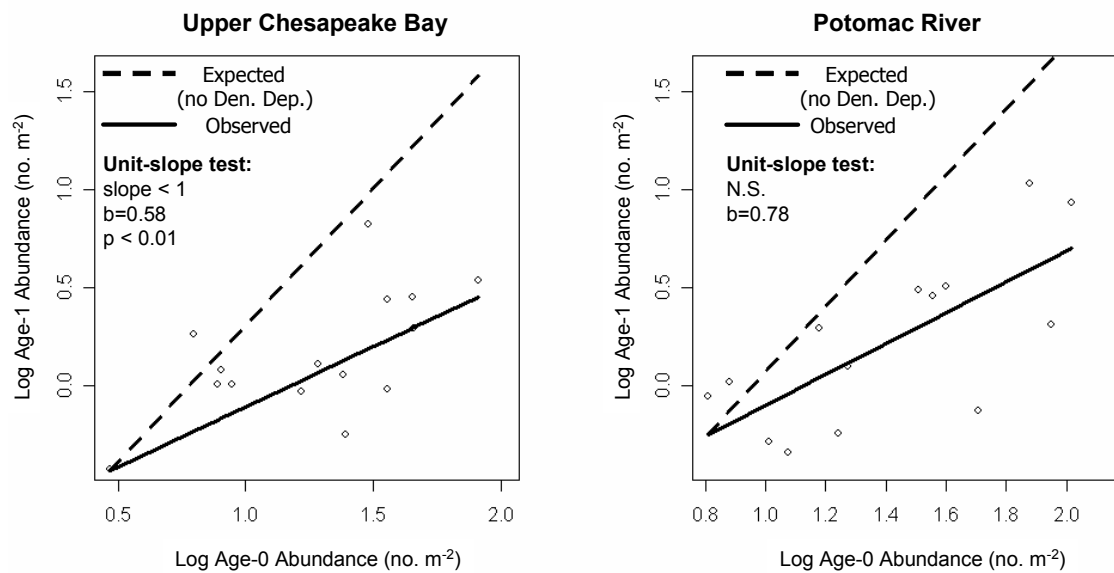


Figure 5-16. Relationship between age-0 striped bass \log_e abundance during first summer and age-1 \log_e abundance the following year in the upper Chesapeake Bay and the Potomac River. Dashed line indicates the expected relationship when mortality rate is constant across all levels of age-0 abundance, i.e., slope = 1. Solid line is fit to observed data. Log-log unit slope test was conducted to test observed data against a slope of 1.

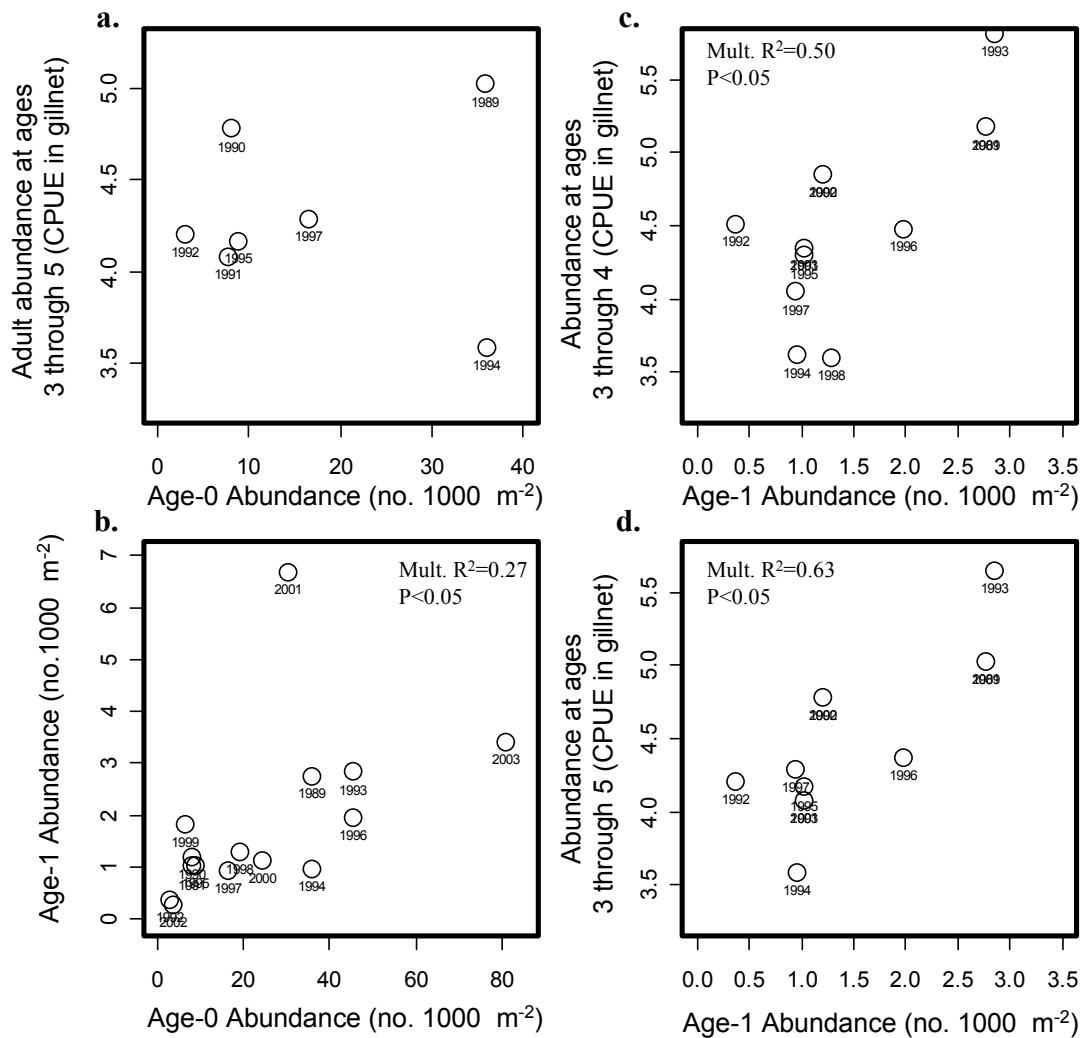


Figure5-17. Relationships between upper Chesapeake Bay striped bass year-class abundance at different ages including a) year class abundance at age-0 and averaged abundance across ages 3-5, b) relationship between abundance at age 0 and abundance at age 1, c) relationship between age-1 abundance and averaged abundance across ages 3- 4, and d) relationship between age-1 abundance and averaged abundance across ages 3-5. Years in the analysis were selected based on availability of abundance data from MD DNR gillnet surveys.

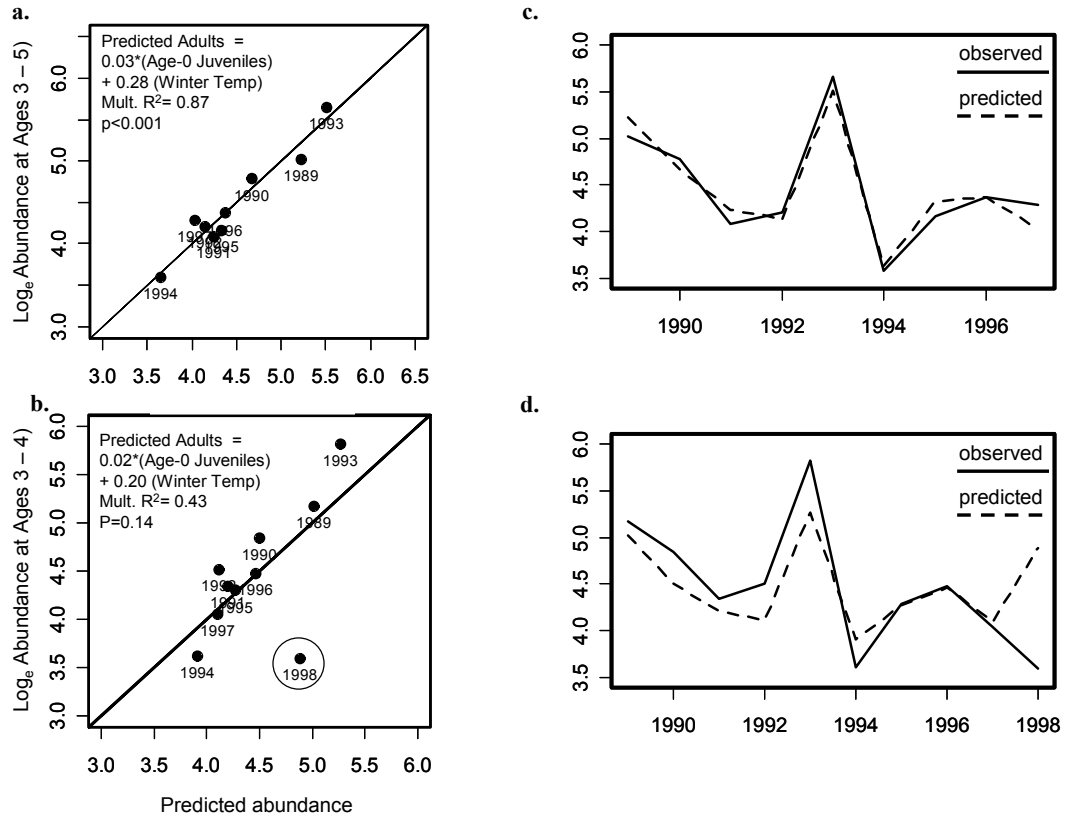


Figure 5-18. Relationship between observed and predicted upper Chesapeake Bay striped bass year-class abundance at ages 3-5 for years 1989-1997 (a and c) and at ages 3-4 for years 1989-1998 (b and d). Included years were selected based on the availability of abundance data from the MD DNR gillnet surveys.

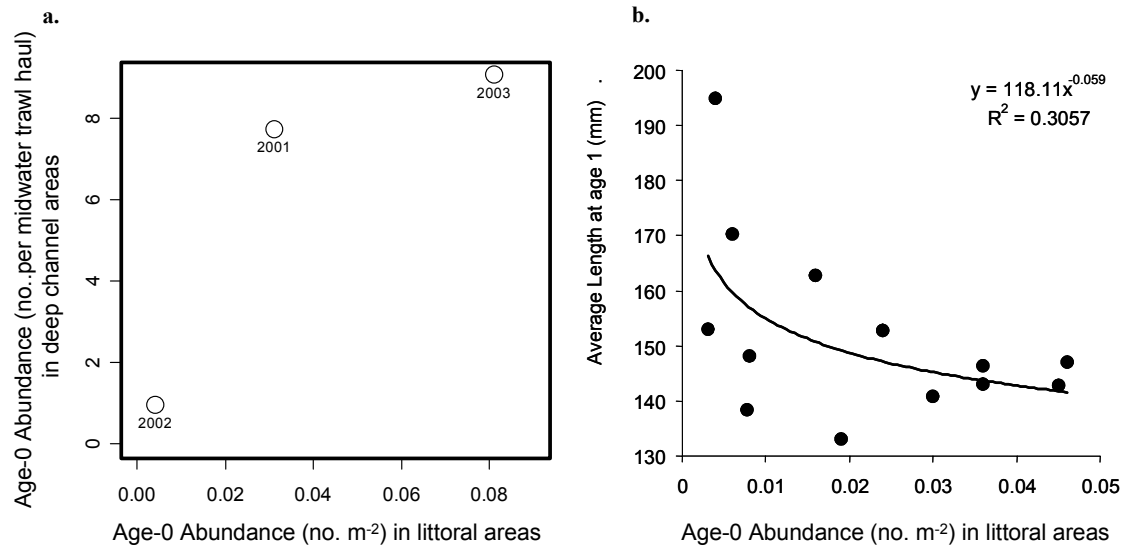


Figure 5-19. Relationship between a) upper Bay age-0 striped bass abundance from summer seine sampling in the littoral zone and age-0 abundance from mid-water trawl sampling in deeper channel locations further downbay and b) relationship between age-0 striped bass abundance during summer from seine surveys and the mean length of age-1 juveniles collected in July of the following year.

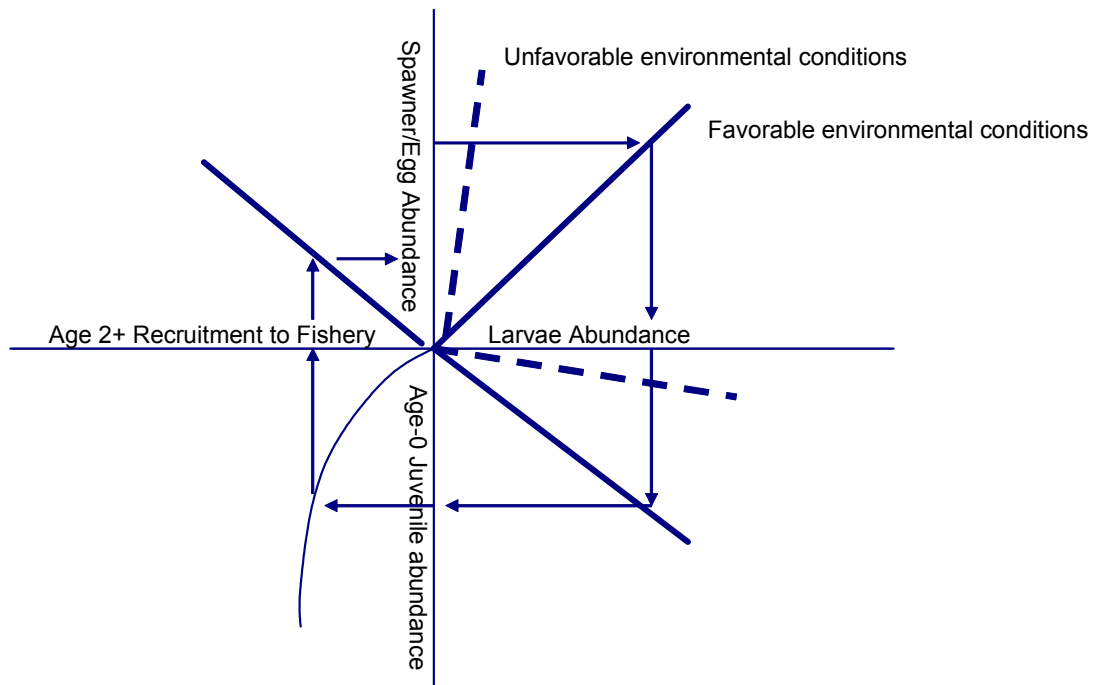


Figure 5-20. Conceptualization of the Chesapeake Bay striped bass recruitment process summarized with a modified Paulik diagram, including both dominant environmental control at the larval stage and strong compensation at the juvenile stage.

CHAPTER SIX

General Summary

Overall Conclusions

Recruitment of striped bass in Chesapeake Bay is subject to coarse control by biophysical mechanisms, including direct and indirect effects of hydrological variability on egg and larval survival (Figure 6-1a). Direct effects are most evident during dry years (e.g. 1999 and 2002) when recruitments of striped bass are poor, whereas indirect effects are evident in years when recruitments are moderate (e.g., years 1998, 2001) and strong (e.g., years 1996, 2003). In dry years, high salinities predominate where yolk-sac and feeding-stage larvae occur and abundances of all larval stages are low, suggesting high egg and yolk-sac larval mortality from down-estuary loss or confinement in unfavorable habitat (i.e. osmotic stress). Indirect effects of hydrological variability are prominent in wet years and operate via trophodynamic processes in which spatial and temporal matches or mismatches with zooplankton prey have consequences for larval feeding success, growth, and survival.

Direct and indirect effects of biophysical controls were not mutually exclusive determinants of recruitment success. Rather, a combination of direct and indirect effects in the egg and larval stages determined coarse levels of recruitment in all years. Favorable transport and retention in the ETM region appear to be necessary but not sufficient to produce the strongest year classes (e.g., 1996, 2003). Strong year classes are associated with high probability of retention of eggs and yolk-sac larvae in the

ETM region (i.e. direct effects) as well as a high degree of spatial and temporal overlap between feeding larvae and prey (i.e. indirect effects).

Inter-annual differences in age-0 to age-1 juvenile mortality rates reduce variability in year-class strength of Chesapeake Bay striped bass (Figure 6-1b). Age-0 juvenile striped bass exhibited density-dependent growth in 5 of the 6 Chesapeake Bay sub-populations that were analyzed. In the upper Bay, density-dependent mortality also was detected. A long juvenile stage duration, regulated by density-dependent growth, if combined with size-selective mortality, can generate high cumulative mortality and act as a strong regulator of year-class strength. Mortality rates of age-0 striped bass in the upper Bay ranged from 0.006 d^{-1} to 0.009 d^{-1} in low- and high-abundance years, respectively. Those rates alone are sufficient to generate a 3-fold difference in survival during the first year of life.

Chapter 2 Summary

The spring ichthyoplankton assemblage in upper Chesapeake Bay exhibited conspicuous inter-annual variability in response to differing hydrological conditions and effects of those conditions on constituent taxa. Taxa that dominated assemblages differed among years, e.g., alosines dominated in 2001 but moronids dominated in 2003; and, the low ichthyoplankton abundance in 2002 was characterized by common occurrence of cyprinid larvae.

Hydrological conditions and the degree that larvae are associated with the ETM and salt front play significant roles in determining recruitment success of anadromous fishes in the upper Bay. Annual differences in distributions of taxa

relative to the ETM and salt front were modulated by freshwater flow levels. Larval distributions are related to larval abundances and apparent survival. For example, the highest summer abundances of age-0 juvenile striped bass and white perch occurred in 2003 when 1) spring conditions were wet, 2) the center of abundance of feeding-stage larvae was within the ETM, and 3) yolk-sac and feeding-stage larval occurrences were lowest below the salt front and ETM. Feeding-stage larvae of anadromous fishes probably benefit from enhanced feeding conditions in high-discharge years.

Abundance of feeding-stage larvae was correlated with age-0 juvenile abundance two months later for all anadromous fish taxa in the three years encompassed by this research. Results indicate that anadromous fish recruitment patterns are at least partly controlled by biophysical processes, i.e., enhanced larval retention and increased spatial overlap with prey set up by annual variability in spring, and possibly late-winter, weather patterns.

Chapter 3 Summary

In a synthesis of six years of data, there was a conspicuous link between hydrological conditions and recruitment of YOY striped bass in upper Chesapeake Bay. YOY striped bass recruitment levels varied >11-fold in the years examined, with lowest recruitment in 2002 and highest in 1996 when mean numbers of juvenile striped bass in the Maryland juvenile index surveys were 1.35 and 15.00 per seine haul, respectively. March and April freshwater flows during the same six years varied more than two-fold.

A multiple regression model successfully described the time series of abundance of four-month old, YOY striped bass for 1985 to 2003 ($r^2 = 0.72$) and successfully forecasted pre-recruit abundance levels for years 2004-2007. A suite of abiotic and biotic variables was considered in the initial model, but only spring freshwater flow and spring temperature were retained as significant ($p < 0.05$) in the final model. The model forecasted pre-recruit abundances within $\pm 30\%$ (median average percent error) of observed levels.

Spatial and temporal controls of prey availability explain the significant effects of spring freshwater flow and temperature in modeled recruitments. Strong recruitments depend on high concentrations of dominant zooplankton prey *Eurytemora affinis* and *Bosmina longirostris*, and require matches of prey and larval striped bass in space and time. In Chesapeake Bay, precipitation and freshwater flow can control the magnitude and distribution of primary production (Adolf et al., 2006), the abundance and distribution of *E. affinis* (Kimmel and Roman, 2004; Lloyd, 2006), and the distribution of striped bass larvae (Chapter 3; (Martino and Houde, 2004) (North and Houde, 2006).

My research is not the first to recognize a positive relationship between freshwater flow and striped bass larval-stage survival or YOY recruitment success in Chesapeake Bay (Boynton, 1976; Ulanowicz and Polgar, 1980; McGovern and Olney, 1996; North and Houde, 2001; Wood, 2000; North and Houde, 2003). My results confirm the relationship and offer a mechanism to explain it. Effect of freshwater flow on larval distributions was analyzed under varying hydrological conditions, and incorporated into statistical models to develop predictive relationships. My findings

provide strong evidence that elevated prey availability, and a high degree of spatial and temporal overlap between zooplankton prey and striped bass larvae, occur in years when YOY recruitment levels are high.

The propensity for occurrence of striped bass larvae to peak near or in the ETM and salt front during strong recruitment years suggests a connection between freshwater flow, the ETM, and striped bass recruitment. Recruitment strength was >10 times higher in 1996 and 2003 than in 1999 and 2002, when most larvae occurred in the ETM (Martino and Houde, 2004), and when ETM conditions were favorable for larval survival (North and Houde, 2003; Martino et al., 2006; North and Houde, 2006). The hypothesized benefit of an increase in prey overlap in wet, strong recruitment years was supported by observed higher feeding success by larvae when freshwater discharge is above average.

Chapter 4 Summary

Growth rates and growth-rate variability of larval-stage striped bass, and sources of the variability were estimated in three years (2001, 2002, 2003) when YOY recruitment varied >9-fold. It was hypothesized that growth would be faster in 2003, an exceptional recruitment year, and that surviving larvae would have grown faster and been larger-at-age compared to average individuals sampled at earlier dates from the larval population.

Exponential growth models provided reasonable fits to larval length-on-age relationships in 2001 and 2003. Growth-in-length rates increased appreciably with larval age in 2003 but increased only slightly with age in 2001. Weight-specific

growth rates (G) between 5dph and 10 dph (first-feeding stage) were similar in 2001 (0.20 d^{-1}) and 2003 (0.19 d^{-1}). However, in the period 10-15 dph, G declined to 0.18 d^{-1} in 2001 but increased rapidly to 0.27 d^{-1} in 2003. Consequently, at 20 dph, larvae were 56% heavier in 2003.

Results supported the hypothesis that larval growth is enhanced in high freshwater-flow years when feeding conditions are favorable. Growth rate was 58% higher in 2003 when average length-specific growth rate was 0.038 d^{-1} compared to 0.024 d^{-1} in 2001. Mean length at 20 dph was 9.30 mm in 2003 but only 8.39 mm in 2001. Growth rates and sizes of three larval survivors sampled in 2002, a year of poor larval production, fell within the ranges observed in 2001 and 2003. Growth-rate variability and associated stage-based mortality could explain the strong 2003 year class of striped bass. Estimated time to reach 9.0 mm was 19.2 days in 2003 but 23.0 days in 2001, based on mean growth rates. Striped bass larvae, if exposed to a typical mortality rate of 0.27 d^{-1} in each year, would have suffered an additional 63% cumulative mortality in the 3.8 additional days required to reach 9.0 mm in 2001.

Differences in growth of larvae between 2001 and 2003 were primarily a result of inter-annual variability in prey availability rather than effects of temperature or maternal investment. Larval feeding success was substantially higher in 2003 when prey concentrations were high. The percentage of small larvae ($< 7.5 \text{ mm}$) that had successfully fed was higher in 2003 (91%) than in 2001 (35%).

Growth patterns of survivors relative to the average larval population supported the hypothesis that surviving larvae were individuals that had grown faster and were larger-at-age than larvae in the average population. These results indicated

selection for fast-growing or larger individuals. The differences between survivors and average larvae were not apparent until larvae were >10 dph in both years, indicating that selection was for differences in growth rather than size at hatching.

Taken together, the combined factors of freshwater flow, zooplankton prey availability, and larval growth provide a mechanism for bottom-up control of recruitment in striped bass. Results support other research on fish early-life stages in the Chesapeake Bay's ETM region that described how apparent behavior, zooplankton prey availability, light, and physical zones of retention can interact to affect survival of larval striped bass and white perch (Shoji et al., 2005; North and Houde, 2006). The new findings reported here identify, describe, and quantify specific mechanisms related to physical and biological controls in the ETM region that enhance growth and survival of striped bass larvae.

Chapter 5 Summary

Strong evidence for density-dependent growth was detected at the age-0 juvenile stage in all except one of the six sub-populations of Chesapeake Bay striped bass considered in this study. Lengths of age-0 juvenile striped bass in late summer were inversely related to abundance. The relationship was described by a negative power model, demonstrating that lengths declined fastest as juvenile abundance increased from low to moderate levels. The results reveal that strong density dependence in growth begins early in the juvenile stage and explains the negative relationship between year-class strength and juvenile size attained.

In years of moderate and high abundance of age-0 juveniles, consumption demand may exceed prey supply. In a synthesis analysis of data available from 1989-2003, maximum densities of YOY striped bass at some sites in the upper Bay reached 0.47 m^{-2} during summer and mean numerical benthic prey densities were 674 m^{-2} . In 2003, when striped bass were most abundant, 0.07 g m^{-2} of polychaete and amphipod prey were available. Based on a bioenergetics model, population-level consumption demand of striped bass juveniles in 2003 reached $0.08 \text{ g m}^{-2} \text{ d}^{-1}$ at sites with highest fish density, exceeding the average standing stock of prey.

The bioenergetics model and the growth-abundance relationships suggested that growth of YOY striped bass in the upper Bay is prey-limited during most years. Observed growth of YOY striped bass was below modeled growth potential in all but two of 15 years, 1995 and 2002, when juvenile abundances were very low. Furthermore, the bioenergetics analysis indicated that temperature differences could not account for inter-annual variability in growth of YOY striped bass in the Bay.

Density-dependent growth was associated with density-dependent juvenile mortality, providing a strong regulatory mechanism on recruitment level of striped bass. In upper Chesapeake Bay and most tributaries, length attained by YOY striped bass at the onset of winter was inversely related to abundance. A statistical model that included an interaction term for juvenile length and winter water temperature explained a substantial amount of the variability ($p < 0.01$, $r^2 = 0.62$) in juvenile mortality rates between the first and second summer of life. Small mean size at the onset of winter and low winter temperatures increase the vulnerability of YOY cohorts to overwinter mortality.

The inter-annual variability in age-0 to age-1 mortality rates could serve to regulate year-class strength of Chesapeake Bay striped bass. For example, mean mortality rates were 0.006 d^{-1} in low-abundance years and 0.009 d^{-1} in high-abundance years. Juvenile striped bass dying at those rates could experience a 3-fold difference in survival during the first year of life. Observed abundances of striped bass that varied >11-fold at age-0 can be reduced to 3-4-fold when a year class recruits to the fishery at age-3.

Density dependence, although not unexpected, had been largely overlooked in earlier research. Findings reported herein offer new insights into the recruitment process of striped bass and potentially other anadromous fishes. A re-evaluation of existing individual-based models (Cowan et al., 1993), and development of new process-oriented simulation models that include both density-independent and density-dependent effects will advance understanding of mechanisms that generate recruitment variability in striped bass. Present results also could be used to improve forecasting capabilities of statistical models by accounting for density-dependent juvenile mortality, and its effects on levels of recruitment of striped bass to the coastwide fishery. A statistical model developed here to model recruitment of striped bass at age 3-5 years includes age-0 abundance, which is an index of larval survival, and winter temperature, an important controller of juvenile survival. The model provided a good fit ($r^2=0.93$) to recruited abundances of striped bass in upper Chesapeake Bay. Such models have potential to be modified and developed as tools to forecast recruitment of striped bass, at least for the fraction of the coastwide stock that is produced in Chesapeake Bay.

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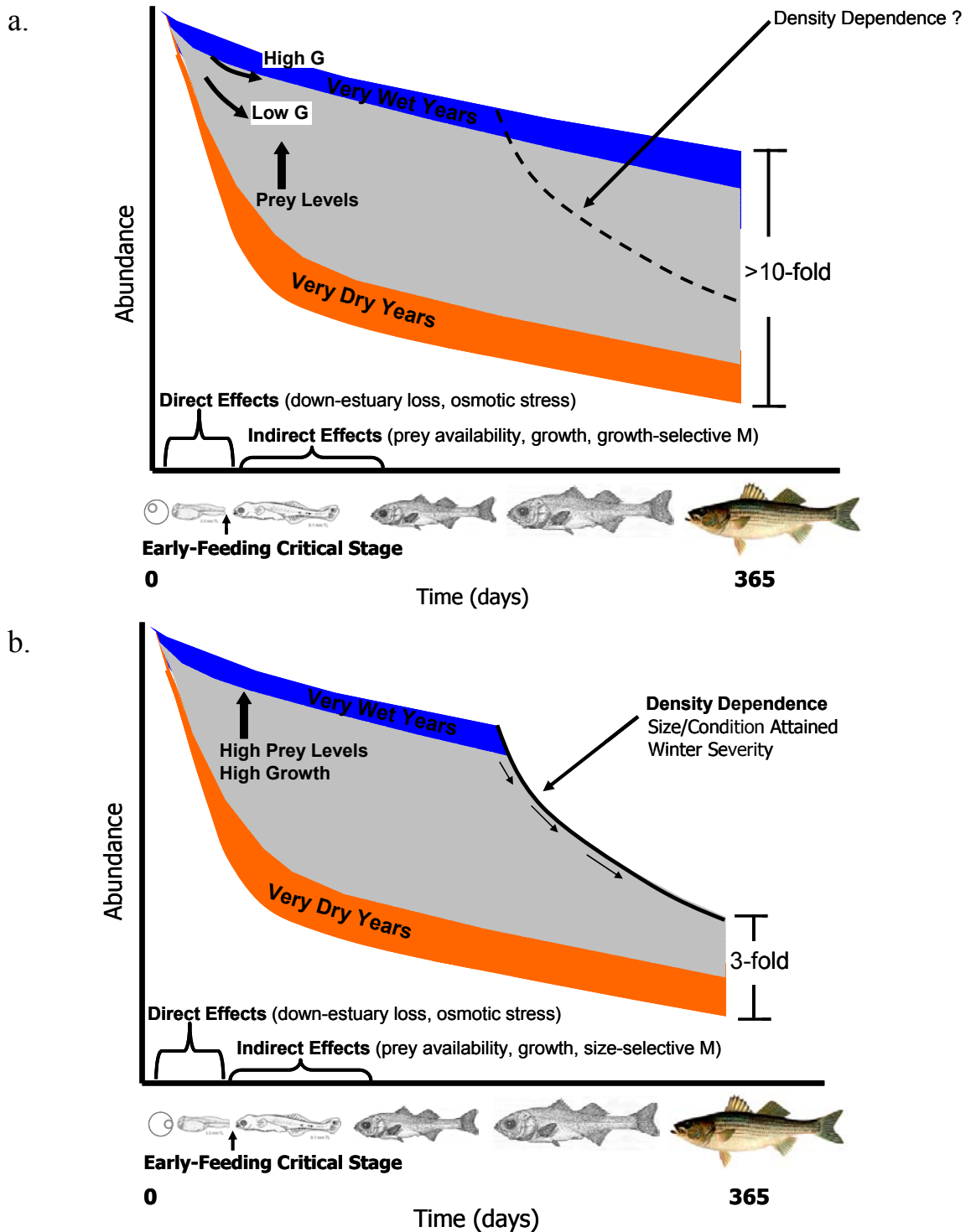


Figure 6-1. Conceptual illustration of controls of annual cohort abundance in Chesapeake Bay striped bass a) without and b) with age-0 juvenile-stage density dependent growth and mortality acting as a regulator of year class strength.

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